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Polypores and genus concepts in Phanerochaetaceae (Polyporales, Basidiomycota)

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Abstract

We explored whether DNA-phylogeny-based and morphology-based genus concepts can be reconciled in the basidiomycete family Phanerochaetaceae. Our results show that macromorphology of fruiting bodies and hymenophore construction do not reflect monophyletic groups. However, by integrating micromorphology and re-defining genera, harmonization of DNA phylogeny and morphological genus concepts is possible in most cases. In the case of one genus (*Phlebiopsis*), our genetic markers could not resolve genus limits satisfactorily and a clear morphological definition could not be identified.

We combine extended species sampling, microscopic studies of fruiting bodies and phylogenetic analyses of ITS, nLSU and *rpb1* to revise genus concepts. Three new polypore genera are ascribed to the Phanerochaetaceae: *Oxychaete* **gen. nov.** (type *Oxyporus cervinogilvus*), *Phanerina* **gen. nov.** (type *Ceriporia mellea*), and *Riopa* (including *Ceriporia metamorphosa* and *Riopa pudens* **sp. nov.**). *Phlebiopsis* is extended to include *Dentocorticium pilatii*, further species of *Hjortstamia* and the monotypic polypore genus *Castanoporus*. The polypore *Ceriporia inflata* is combined into *Phanerochaete*.

The identity of the type species of the genus *Riopa*, *R. davidii*, has been misinterpreted in the current literature. The species has been included in *Ceriporia* as a species of its own or placed in synonymy with *Ceriporia camaresiana*. The effort to properly define *R. davidii* forced us to study *Ceriporia* more widely. In the process we identified five closely related *Ceriporia* species that belong to the true *Ceriporia* clade (Irpicaceae). We describe those species here, and introduce the *Ceriporia pierii* group. We also select a lectotype and an epitype for *Riopa metamorphosa* and neotypes for *Sporotrichum aurantiacum* and *S. aurantium*, the type species of the anamorphic genus *Sporotrichum*, and recommend that teleomorphic *Riopa* is conserved against it.

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Key words
Systematics, taxonomy, morphology, anamorphic fungi

Introduction

Fruiting bodies are the most visible and easily studied element of the life cycle of macrofungi. Fruiting body morphology, including overall shape and construction of the spore-producing surface (hymenophore in basidiomycetes), was adopted early on as the guiding principle of fungal classification. This practical, but artificial, system has been largely replaced by a more natural, phylogenetic classification based on molecular characters (Hibbett et al. 2007, McLaughlin and Spatafora 2014, 2015).

At higher levels, there is rampant convergence and parallelism in the evolution of fruiting body and hymenophore types, possibly with a general trend towards evolution of more complex types. For instance, some orders of basidiomycetes only contain simple, effused fruiting bodies (e.g. Atheliales, Corticiales), while others are dominated by more complex forms (e.g. Agaricales, Gloeophyllales). Nevertheless, fruiting body morphology and hymenophore type remain significant for classification of fungi, particularly at very low taxonomic levels (e.g. within genera). The separate research traditions of specialists on morphological groups such as agarics, corticioid fungi and polypores have hindered comparisons of morphologically distinct yet closely related taxa. Otherwise well implemented studies for instance in polypore systematics sometimes neglect closely related corticioid fungi (Li and Cui 2013, Jia et al. 2014, Chen et al. 2015).

A number of studies have shown that hymenophore types classified separately may actually belong to the same genus. Examples include *Hyphodontia/Xylodon* (Langer 1994, Larsson et al. 2007), *Resupinatus* (Thorn et al. 2005), *Schizophyllum* (Nakasone 1996), *Sidera* (Miettinen and Larsson 2011), *Steccherinum* (Miettinen et al. 2012), and *Trechispora* (Larsson 1994, Larsson et al. 2011, Birkebak et al. 2013). In the present study we explore whether phylogenetic genus-level classification and hymenophore type based classification can be united into a coherent system in the family Phanerochaetaceae.

Larsson (2007) suggested the adoption of Phanerochaetaceae for a clade of corticioid fungi around the genus *Phanerochaete*. A more comprehensive sampling of the Polyporales by Binder et al. (2013) suggests that Phanerochaetaceae is indeed a well-supported subclade of the large phlebioid clade, with the polypore genus *Bjerkandera* as the sister clade to the rest of the family. The family, as well as others mentioned in this paper, will also be adopted in the forthcoming treatment of Polyporales systematics by Justo et al. (in preparation). Aside from *Bjerkandera*, all the members of the Phanerochaetaceae identified in previous analyses have been corticioid or hydnoid fungi, most of them simple septate and monomitic, with the exception of *Hapalopilus*, a polypore genus with clamped hyphae. Here we describe two new polypore genera for the family (Figure 1).

Figure 1. Fruiting body diversity in Phanerochaetaceae. **a** *Phlebiopsis castanea* (=*Castanoporus castaneus*), Russia, Spirin 5704 **b** effused polypore *Phanerina mellea*, Indonesia, Miettinen 11393 **c** corticioid *Phlebiopsis pilatii*, Russia, Spirin 6268 **d** polypore *Riopa metamorphosa* intermixed with its anamorphic stage *Sporotrichum aurantiacum*, Czech Republic, Vlasák 0511/15. Photos taken in the field.

The corticioid members of the Phanerochaetaceae have been popular subjects of phylogenetic research, which has resulted in revision of genus concepts within the family. Greslebin et al. (2004) created the new genus *Rhizochaete* for pigmented *Phanerochaete*-like taxa in a separate clade within the Phanerochaetaceae. Wu et al. (2010) produced an extended phylogeny of the Phanerochaetaceae, extending the genera *Hjortstamia* and *Phlebiopsis*. The most comprehensive phylogenetic treatment until now, produced by Floudas and Hibbett (2015), resulted in creation of *Phaeophlebiopsis* for *Phlebia*-like taxa

that are phylogenetically separated from the similar *Phlebiopsis* species, and moved a species of *Hjortstamia* to *Phlebiopsis*. Chikowski et al. (2016) extended the genus *Rhizochaete* further, including species with inconspicuous, poorly differentiated cystidia.

As a result of these and other (De Koker et al. 2003, Hallenberg et al. 2008) studies, Phanerochaetaceae contained 8–9 genera of corticioid fungi at the onset of this study (*Donkia*, *Hyphodermella*, *Phaeophlebiopsis*, *Phanerochaete*, *Phlebiopsis*, *Pirex*, *Rhizochaete*, *Terana* and probably *Porostereum*). Looking at species numbers, Phanerochaetaceae is heavily dominated by corticioid fruiting body types. The polypore genera *Bjerkandera* and *Hapalopilus* are neatly separated from corticioid species.

To better understand the morphological variation and evolution within the Phanerochaetaceae, we have incorporated new species — polypores and corticioid fungi — to the datasets published by earlier authors. With this new data we provide an updated phylogeny of the family, and revise species concepts therein.

Methods

DNA and phylogenetics

We produced 36 new nuclear ribosomal DNA internal transcribed spacer (ITS) sequences, 20 large subunit (nLSU, 28S) sequences, and 4 RNA Polymerase II Largest Subunit (*rpb1*) sequences. They have been deposited in the INSDC (Cochrane et al. 2016) under the accession numbers KX752590–KX752629. We also used ITS, nLSU and *rpb1* sequences of 99 specimens retrieved from the INSDC (Suppl. material 1 – INSDC accession numbers), chosen based mainly on previous studies (Wu et al. 2010, Binder et al. 2013, Floudas and Hibbett 2015, Volobuev et al. 2015).

Various DNA extraction methods were used: standard chloroform extraction (Murray and Thompson 1980), E.Z.N.A. forensic DNA kit (Omega Bio-Tek, Norcross, GA, USA), and DNeasy plant mini kit (Qiagen, Hilden, Germany). PCR primers included ITS1F, ITS5, ITS1, ITS4 and LR22 for the ITS; CTB6, LR0R and LR7 for the partial nLSU (http://biology.duke.edu/fungi/mycolab/primers.htm); and RPB1-Af and RPB1-Cr for *rpb1* (Matheny et al. 2002). Sequencing primers were the same with the addition of primers LR5 and LR3R for nLSU and RPB1-Int2.2f (Binder et al. 2009) for *rpb1*.

We compiled three datasets for phylogenetic analyses:

1. LSU-dataset of the phlebioid clade (Irpicaceae, Meruliaceae, Phanerochaetaceae) based on nuclear ITS and LSU sequences, with 122 specimens. Of these, 100 had ITS and 118 nLSU sequence available. Total alignment length after manually removing unalignable characters was 1799 bp with 474 (26%) parsimony informative characters. The tree was rooted with *Phlebia radiata* (Meruliaceae).
2. *Rpb1*-dataset for Phanerochaetaceae based on *rpb1*, ITS and nLSU sequences with 34 species, all containing all three genetic markers. Total alignment length after re-

moving unalignable characters was 3064 bp with 672 (22%) parsimony informative characters. The tree was rooted with *Bjerkandera adusta*.

3. *Hapalopilus* dataset with 16 ITS sequences, with a total alignment length 593 bp and 20 (3%) parsimony informative characters. The tree was rooted with *H. percoctus* (described in this paper).

Sequences were aligned using MAFFT online versions 7.233-7.244 with strategy E-INS-I (http://mafft.cbrc.jp, Katoh and Standley 2013) and adjusted manually using PhyDE 0.9971 (Müller et al. 2010). Numbers of informative characters were calculated in MEGA6 (Tamura et al. 2013).

We used MrBayes 3.2 (Ronquist et al. 2012) for inferring Bayesian consensus trees for the three datasets. The LSU and *rpb1* datasets were partitioned as follows: ITS1 and ITS2 in one partition, 5.8S and LSU in another, and *rpb1* separately. The nucleotide substitution model GTR+I+G was used for all partitions except *Hapalopilus* ITS, for which GTR was used. Models were chosen based on AIC scoring produced in jmodeltest (Darriba et al. 2012). Bayesian analyses were run with eight chains in three parallel runs, temp=0.1. LSU dataset was run for 10 (LSU dataset), 2 (*rpb1*) and 4 (*Hapalopilus*) million generations sampling every 2000 generations. All runs converged to below 0.01 average standard deviation of split frequencies. A burn-in of 25% was used before computing the consensus tree.

In parallel with the Bayesian analyses, we used RAxML 8.1.3 (Stamatakis 2014) for maximum likelihood inference and bootstrapping, partitioned similarly as in Bayesian analysis but using the GTR+G substitution model for all datasets. The tree with the highest likelihood from 100 individual runs was selected, and bootstrap values were calculated from 1000 repetitions. All the phylogenetic analyses were done at the CSC – IT Center for Science (https://www.csc.fi) multi-core computing environment. The resulting phylograms were pre-edited in FigTree 1.4.2 (Rambaut 2014) and processed further in CorelDRAW X6. Since the Bayesian and maximum likelihood analyses had similar topologies in all well-supported and relevant nodes, we report here only the Bayesian results amended with bootstrap support values from the maximum likelihood analyses. The alignments and phylograms are available in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S19710).

Microscopy

We used a Leica DMLB microscope with optional phase contrast illumination for microscopic observations. Basic mountant was Cotton Blue (CB, Merck 1275) made in lactic acid, but we also used Melzer's reagent (IKI), 5% KOH, and Cresyl Blue (CRB, Merck 1280). Sketches were made using a drawing tube with the exception of spores that were drawn with free hand after a real measured spore. The sketches were then imported to CorelDRAW X6 and converted to vector graphics. Spore statistics were produced with R version 3.0.2 (R Core Team 2013).

In microscopic descriptions, the following abbreviations are used: L – mean spore length, W – mean spore width, Q – L/W ratio. Entry CB+ means cyanophily, CB– acyanophily; IKI– means neither amyloid nor dextrinoid reaction. While reporting pore and spore measurements, the whole range is given in parentheses; 90% range excluding 5% extreme values from both ends of variation is given without parentheses; in case the values are identical, parentheses are omitted. For basidial and hyphal width measurements, the 20% tails are in parentheses.

Results

Our phylogenetic analyses support the division of the phlebioid clade into three lineages in line with previous research (Binder et al. 2013, Floudas and Hibbett 2015): Meruliaceae, Irpicaceae (*Byssomerulius* clade in the sense of Larsson 2007) and Phanerochaetaceae (Figure 2). In the analyses of our LSU dataset (ITS+nLSU), the Phanerochaetaceae receives excellent support (posterior probability=1, bootstrap support=98%) and the Irpicaceae good to moderate support (pp=0.97, bs=59%), while the tree was rooted within the Meruliaceae (*Phlebia radiata*).

The Phanerochaetaceae can further be divided into several clades: *Bjerkandera* clade (pp=0.71, bs=57%), *Phanerochaete* clade (pp=1, bs=87%), *Donkia* clade (pp=1, bs=85%), and *Phlebiopsis* clade (pp=1, bs=0.98%) (Figure 2). Support values are similar for the *rpb1*-dataset (ITS+nLSU+*rpb1*, Figure 3). We report polypores in all of these clades except the *Donkia* clade.

The ***Bjerkandera* clade** contains three genera: pileate polypores in the genus *Bjerkandera*, the effused corticioid genus *Terana*, and *Porostereum* spp. with smooth hymenophore and caps. All known species in these genera have clamped septa.

The ***Phanerochaete* clade** contains numerous corticioid species as well as five species of polypores: *Ceriporia inflata*, *Oxychaete cervinogilva* (=*Oxyporus cervinogilvus*), *Phanerina mellea* (=*Ceriporia mellea*), *Riopa metamorphosa* (=*Ceriporia metamorphosa*), and *Riopa pudens*. This clade contains only simple-septate species with one exception (*Phanerochaete krikophora* nom. prov.), whereas clamped and simple-septate species are intermixed in other parts of the Phanerochaetaceae. To create monophyletic genera, we have two options: a wide, morphologically heterogeneous *Phanerochaete* that includes a number of different-looking polypores, or three polypore genera in addition to a more homogenous *Phanerochaete*. We have opted to use three polypore genera: *Oxychaete*, *Phanerina* and *Riopa*. Even after this, a polypore species, *Ceriporia inflata* with incomplete pores, is nested within *Phanerochaete*, where it is closely related and microscopically very similar to spiny species. Nevertheless, this arrangements allows us to stick largely with morphologically identifiable genera (Tables 1 and 2).

Even though somewhat different from *Phanerochaete*, the polypore species in the *Phanerochaete* clade have an uncharacteristically simple hyphal structure for a polypore. They have no hyphal pegs or cystidioles. The subhymenial structure is loose, reminding a cymoid corymb in botanical terms (see Figs 7–9). In contrast, a typical

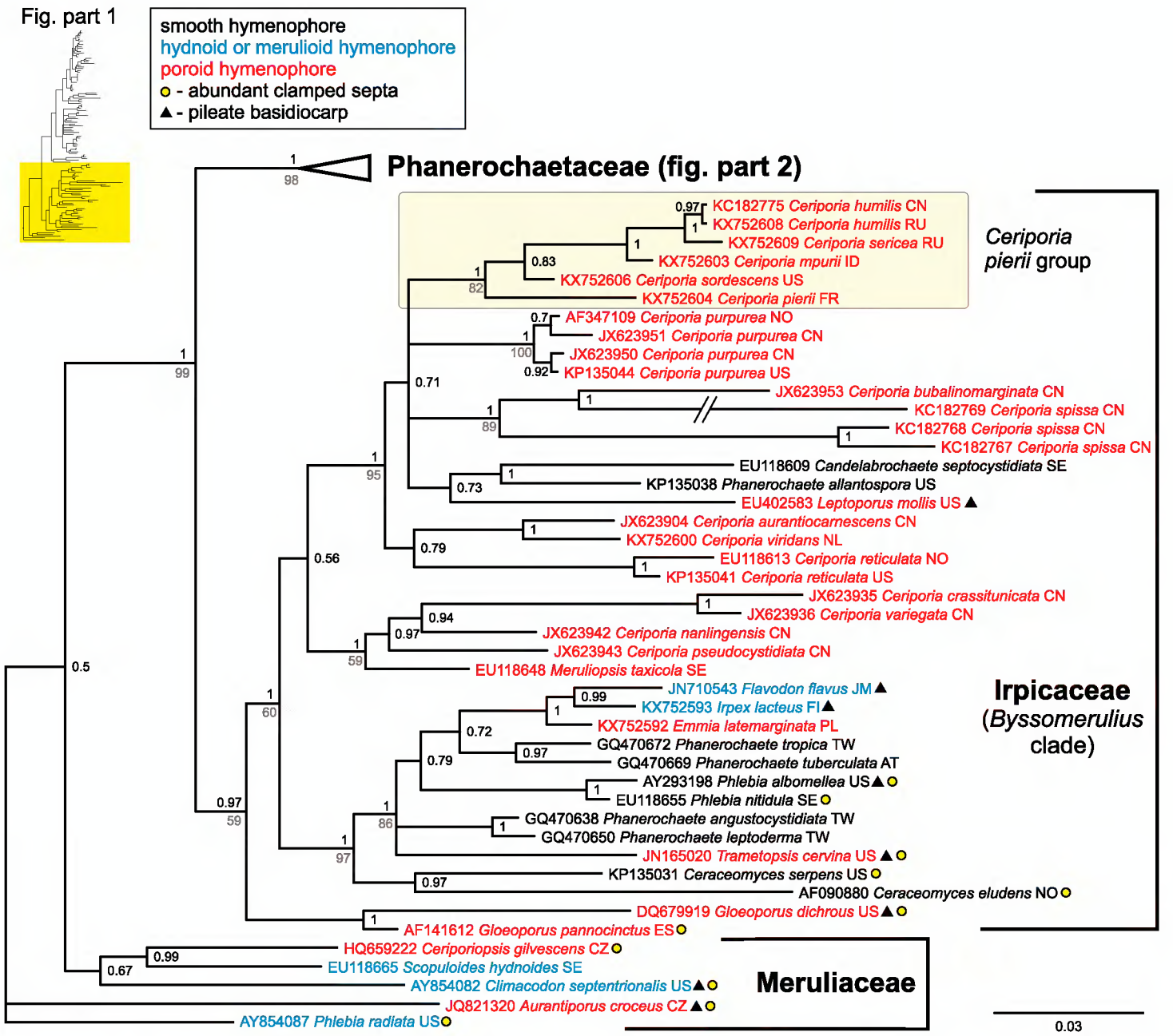
Fig. part 1
smooth hymenophore
hydnoid or merulioid hymenophore
poroid hymenophore
○ - abundant clamped septa
▲ - pileate basidiocarp
Phanerochaetaceae (fig. part 2)
Ceriporia pierii group
KC182775 Ceriporia humilis CN
KX752608 Ceriporia humilis RU
KX752609 Ceriporia sericea RU
KX752603 Ceriporia mpurii ID
KX752606 Ceriporia sordescens US
KX752604 Ceriporia pierii FR
AF347109 Ceriporia purpurea NO
JX623951 Ceriporia purpurea CN
JX623950 Ceriporia purpurea CN
KP135044 Ceriporia purpurea US
JX623953 Ceriporia bubalinomarginata CN
KC182769 Ceriporia spissa CN
KC182768 Ceriporia spissa CN
KC182767 Ceriporia spissa CN
EU118609 Candelabrochaete septocystidiata SE
KP135038 Phanerochaete allantospora US
EU402583 Leptoporus mollis US ▲
JX623904 Ceriporia aurantiocarnescens CN
KX752600 Ceriporia viridans NL
EU118613 Ceriporia reticulata NO
KP135041 Ceriporia reticulata US
JX623935 Ceriporia crassitunicata CN
JX623936 Ceriporia variegata CN
JX623942 Ceriporia nanlingensis CN
JX623943 Ceriporia pseudocystidiata CN
EU118648 Meruliopsis taxicola SE
Irpicaceae (Byssomerulius clade)
JN710543 Flavodon flavus JM ▲
KX752593 Irpex lacteus FI ▲
KX752592 Emmia latemarginata PL
GQ470672 Phanerochaete tropica TW
GQ470669 Phanerochaete tuberculata AT
AY293198 Phlebia albomellea US ▲ ○
EU118655 Phlebia nitidula SE ○
GQ470638 Phanerochaete angustocystidiata TW
GQ470650 Phanerochaete leptoderma TW
JN165020 Trametopsis cervina US ▲ ○
KP135031 Ceraceomyces serpens US ○
AF090880 Ceraceomyces eludens NO ○
DQ679919 Gloeoporus dichrous US ▲ ○
AF141612 Gloeoporus pannocinctus ES ○
HQ659222 Ceriporiopsis gilvescens CZ ○
EU118665 Scopuloides hydnoides SE
AY854082 Climacodon septentrionalis US ▲ ○
JQ821320 Aurantiporus croceus CZ ▲ ○
Meruliaceae
AY854087 Phlebia radiata US ○
0.03

Figure 2. Phylogeny of the phlebioid clade of the Polyporales with emphasis on *Ceriporia* clade and Phanerochaetaceae. Bayesian consensus tree based on ITS and nLSU sequences. Figures denote posterior probabilities (figures between 0 and 1) and bootstrap support values of the maximum likelihood analysis (figures between 50 and 100).

polypore subhymenium is more difficult to study, hyphae are tightly interwoven, less clearly oriented and more irregular. Pores of *Phanerochaete* clade polypores are shallow and in many species irregular. Basidiocarps are relatively thin. All cystidia are hymenial, and no cystidia of tramal origin typical for many cystidioid polypores (such as *Rigidoporus*) are present.

The ***Donkia* clade** is a sister to the *Phanerochaete* clade, and contains the genera *Donkia*, *Hyphodermella* and *Pirex* as well as some species ascribed to *Phlebia* sensu lato. It includes smooth to hydnoid, pileate to effused species, many of which have clamped septa and are also otherwise morphologically quite different from *Phanerochaete*.

The ***Phlebiopsis* clade** contains a wide variety of different fruiting body types: pileate polypores with clamped septa (*Hapalopilus*), a resupinate polypore with simple septa (*Phlebiopsis castanea* or *Castanoporus castaneus*), phlebioid taxa with tight, simple-

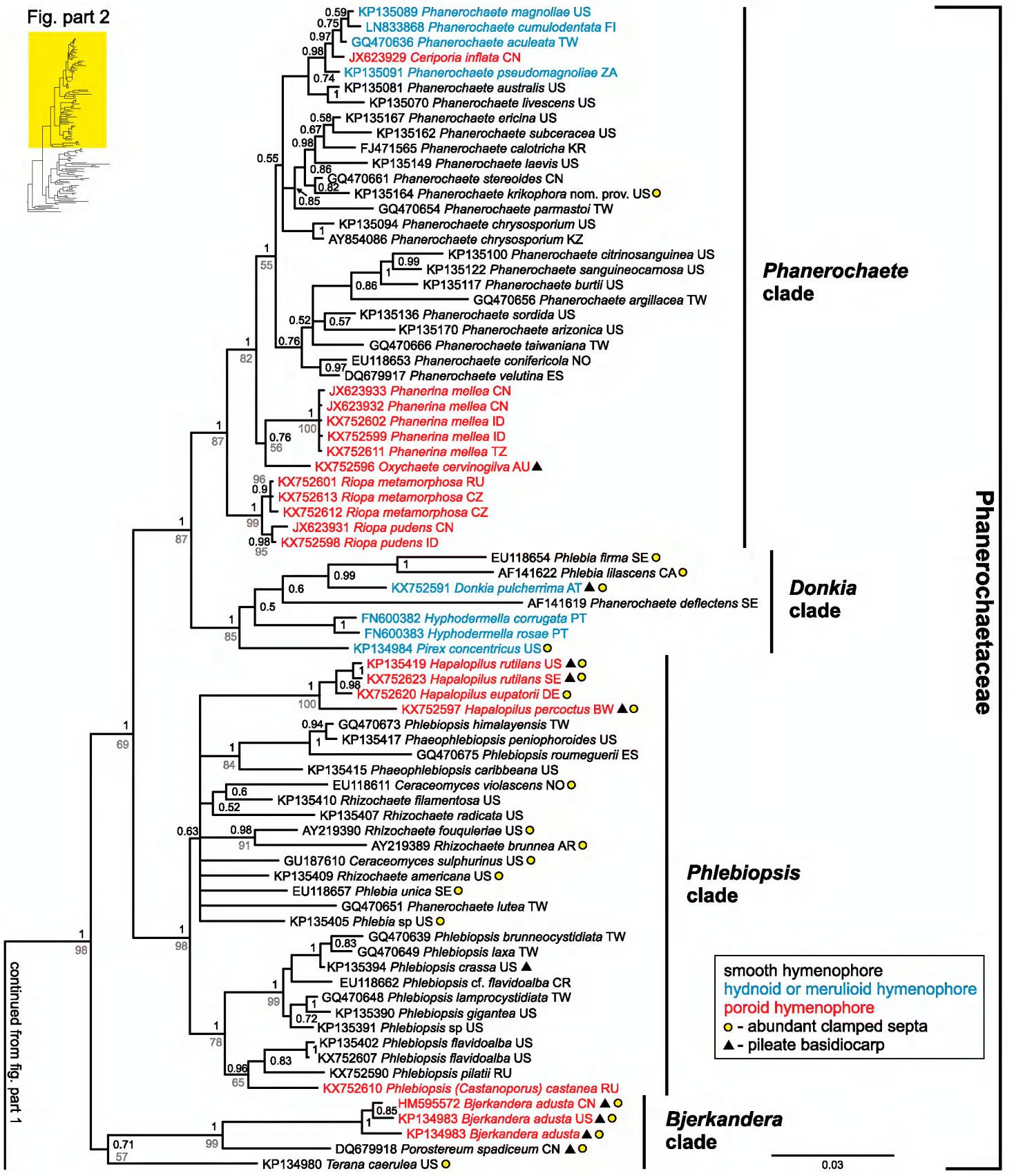

Figure 2. Continued.

septate fruiting bodies and encrusted cystidia (*Phlebiopsis*), and loose rhizomorphic fruiting bodies (*Rhizochaete*). The internal structure of the clade is poorly resolved in the LSU dataset (Figure 2). The *rpb1* dataset (Figure 3) includes too few species to be of much help either at this point. Three clades are well supported — *Hapalopilus*, *Phaeophlebiopsis* and *Phlebiopsis* — but *Rhizochaete* is poly- or paraphyletic. Further species sampling and genes may help the situation, but in our experience poor resolution of nrDNA markers in Polyporales often persists in expanded datasets.

Table 1. Morphological comparison of simple septate corticioid genera of the Phanerochaetaceae.

	Phanerochaete	*Phlebiopsis*	*Phaeophlebiopsis*	*Rhizochaete*	*Hyphodermella*
number of known species	many	>10	3	9	6
spore shape	cylindrical, ellipsoid	cylindrical, ellipsoid	cylindrical, ellipsoid	cylindrical, ellipsoid	ellipsoid
hymenophore	smooth, hydnoid, poroid	smooth, poroid	smooth	smooth	hydnoid
clamps	–*	–	–	+/–	–
subhymenium	loose, corymb like	interwoven	interwoven	interwoven	loose, corymb type
lamprocystidia	–	+	+	+/–	–
basal layer / cap context	not agglutinated	agglutinated/tight	agglutinated/tight	not agglutinated	not agglutinated
colors	pale	pale to brown	pale	many bright-colored or brown	pale to brown
KOH reaction	red or green if present	purple if present	absent	purple if present	absent
rhizomorphs	many species	absent	absent	always present	absent

*present in one species

Table 2. Morphological comparison of simple-septate polypores of the Phanerochaetaceae with similar genera.

	Phlebiopsis	*Oxychaete*	*Phanerina*	*Riopa*	*Oxyporus*	*Emmia*	*Ceriporia*	*Phanerochaete* (core)
number of polypores	1	1	1	2	>10	2	many	1
dry basidiocarp	resupinate, thin	pileate, light board-like	resupinate, rather fragile	resupinate, fragile	tough	resupinate, not particularly fragile	resupinate, fragile	resupinate, rather fragile
color	yellowish brown	yellow-brown	yellow	white-orange	white-cream	white-cream	white-red-purple	light-colored
pores	shallow, large	shallow, large, regular	shallow, large	shallow, medium to large	deep, small to large	deep, medium seized	small to medium	absent/irpicoid
cystidia	thick-walled subulate, encrusted	thick-walled subulate, encrusted	thin-walled subulate, naked	tubular thin-walled, naked	thin- to thick-walled subulate, encrusted; gloeocystidia	cylindrical, thin-walled, encrusted	no (cystidioles)	thin-walled cylindrical (polypore) to thick-walled subulate, often encrusted
encrustation	abundant	only in cystidia	large crystals	large crystals & sticky resin	variable, large crystals, cystidia	scarce, coarse	often abundant, also sticky resin	large crystals, sometimes on cystidia
hyphae	thick-walled throughout, wide	thick-walled throughout, wide	thin- to thick-walled, slightly wider in subiculum	thin- to slightly thick-walled, narrow	narrow, thick-walled	narrow, thin-walled	often wide and inflated in subiculum, thin- to thick-walled	often wide in subiculum, thin- to thick-walled
hyphal consistency	rather dense, subiculum may be loose, basal layer agglutinated	very loose, hyphae straight	trama rather dense, subiculum loose	rather loose	rather dense	rather loose	loose	subiculum loose, subhymenium often dense
hyphal H-connections	no	no	no	no	no	no	yes	yes
hymenium	subhymenium condensed, basidia mid-sized	distinct corymb branching, long basidia	dense but still corymb branching	corymb branching	tight interwoven to looser with inflated cells	subhymenium very short-celled, interwoven, basidia long	subhymenium very short-celled, interwoven, cells often inflated, basidia short	corymb branching
spores	mid-sized (5.5×2.8 µm), cylindrical, slightly curved, thin-walled	large (7×3 µm), cylindrical, slightly curved, thin-walled	large (6.5×3 µm), cylindrical to narrow ellipsoid, walls rather thin but distinct	mid-sized (5–5.5×2–2.5 µm), curved cylindrical	broad ellipsoid to globose, mid-sized to large, slightly thick-walled	narrow ellipsoid, mid-sized (4–6×2.5–3 µm), thin-walled	curved cylindrical to ellipsoid, small to mid-sized, thin-walled	cylindrical to narrow ellipsoid, mid-sized, thin-walled

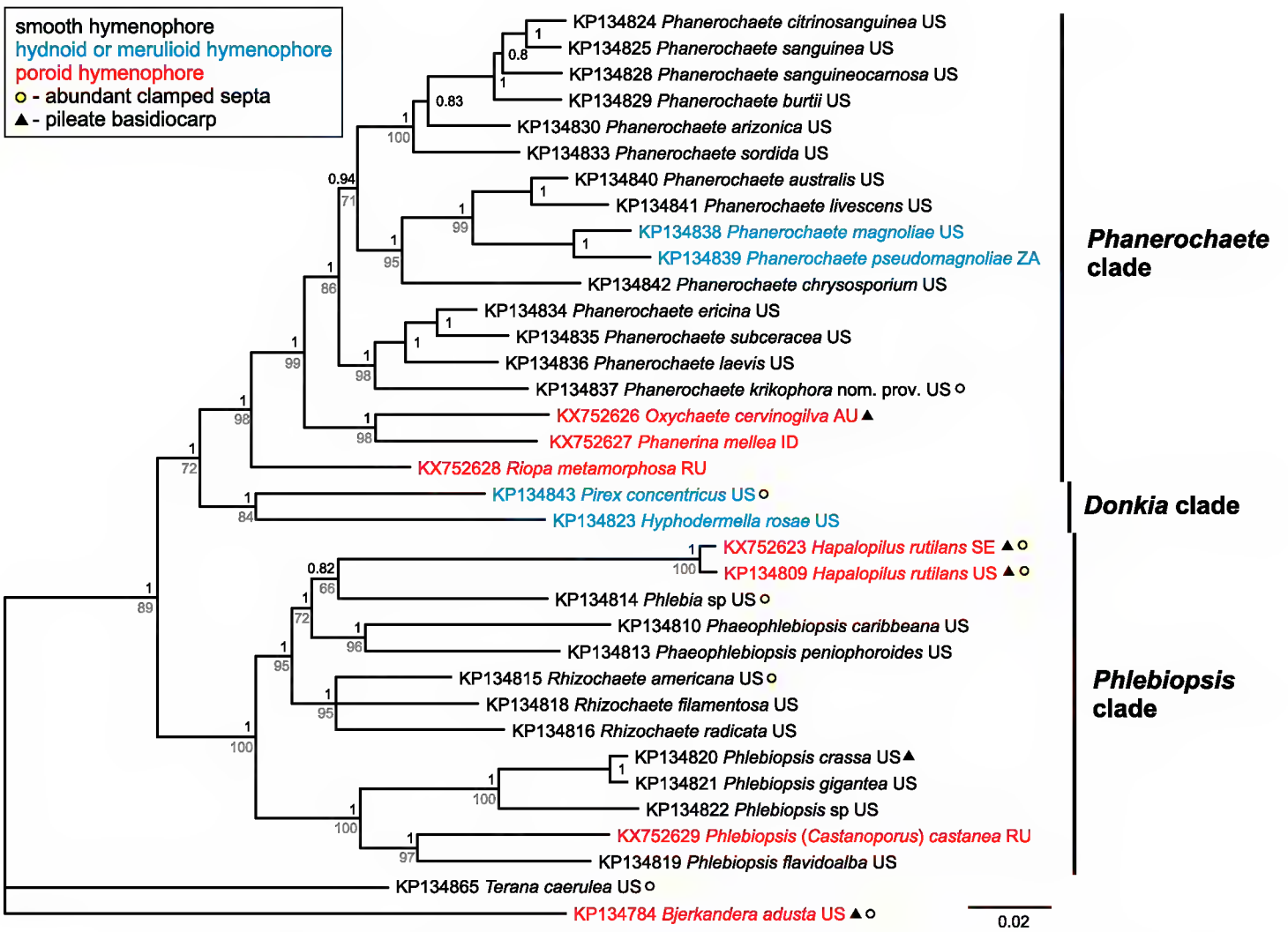
smooth hymenophore
hydnoid or merulioid hymenophore
poroid hymenophore
○ - abundant clamped septa
▲ - pileate basidiocarp
KP134824 Phanerochaete citrinosanguinea US
KP134825 Phanerochaete sanguinea US
KP134828 Phanerochaete sanguineocarnosa US
KP134829 Phanerochaete burtii US
KP134830 Phanerochaete arizonica US
KP134833 Phanerochaete sordida US
KP134840 Phanerochaete australis US
KP134841 Phanerochaete livescens US
KP134838 Phanerochaete magnoliae US
KP134839 Phanerochaete pseudomagnoliae ZA
KP134842 Phanerochaete chrysosporium US
KP134834 Phanerochaete ericina US
KP134835 Phanerochaete subceracea US
KP134836 Phanerochaete laevis US
KP134837 Phanerochaete krikophora nom. prov. US ○
KX752626 Oxychaete cervinogilva AU ▲
KX752627 Phanerina mellea ID
KX752628 Riopa metamorphosa RU
KP134843 Pirex concentricus US ○
KP134823 Hyphodermella rosae US
KX752623 Hapalopilus rutilans SE ▲○
KP134809 Hapalopilus rutilans US ▲○
KP134814 Phlebia sp US ○
KP134810 Phaeophlebiopsis caribbeana US
KP134813 Phaeophlebiopsis peniophoroides US
KP134815 Rhizochaete americana US ○
KP134818 Rhizochaete filamentosa US
KP134816 Rhizochaete radicata US
KP134820 Phlebiopsis crassa US ▲
KP134821 Phlebiopsis gigantea US
KP134822 Phlebiopsis sp US
KX752629 Phlebiopsis (Castanoporus) castanea RU
KP134819 Phlebiopsis flavidoalba US
KP134865 Terana caerulea US ○
KP134784 Bjerkandera adusta US ▲○
Phanerochaete clade
Donkia clade
Phlebiopsis clade
0.02

Figure 3. Phanerochaetaceae phylogeny, Bayesian consensus tree based on ITS, nLSU and *rpb1* sequences. Figures denote posterior probabilities (figures between 0 and 1) and bootstrap support values of the maximum likelihood analysis (figures between 50 and 100).

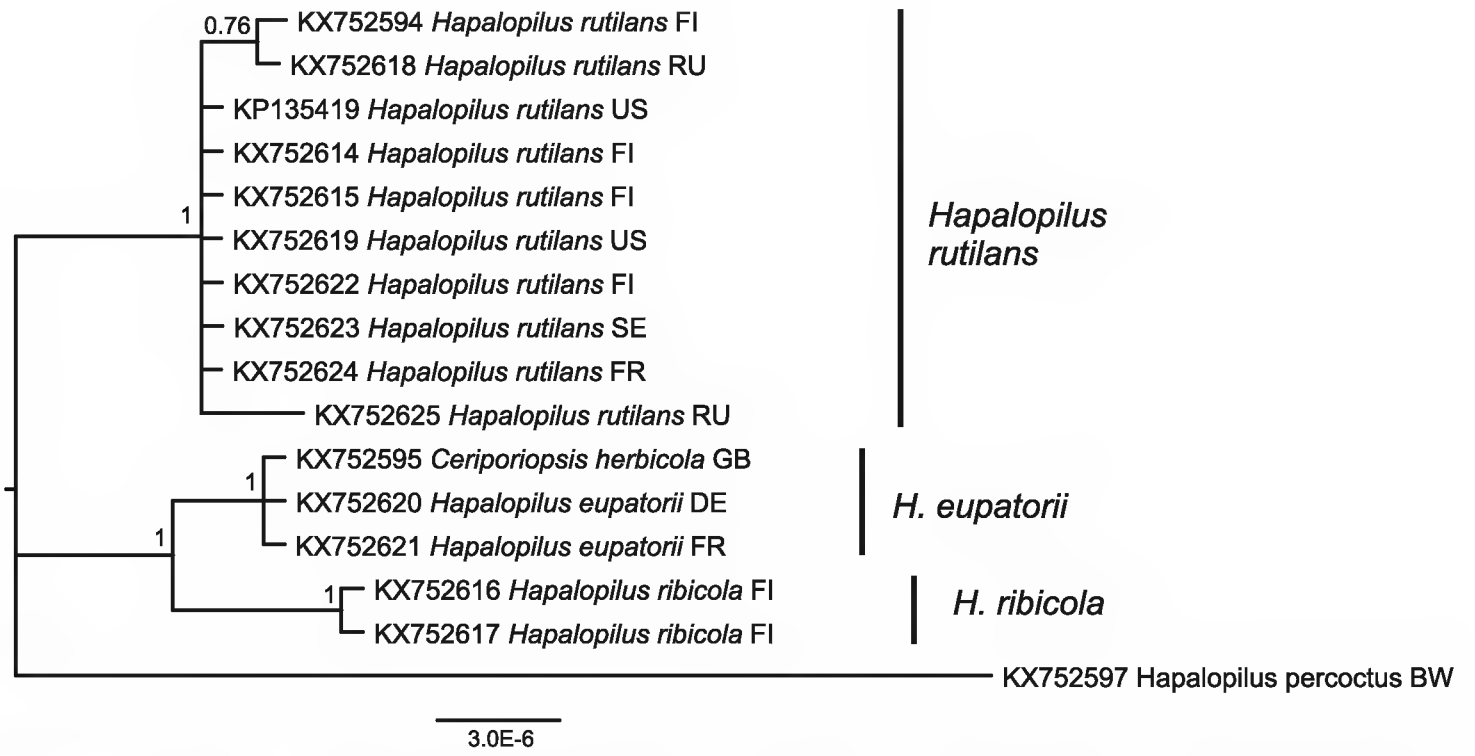

Figure 4. Relations of *Hapalopilus* spp. Bayesian consensus tree based on ITS sequences. Figures denote posterior probabilities.

No intuitively pleasing genus arrangement seems to be in reach for the *Phlebiopsis* clade. Based on our LSU dataset, the only well supported options for including all species in monophyletic genera would be either one genus for the whole clade (for which *Hapalopilus* has priority), or 10–13 separate genera, most of them new and monotypic. Neither is a satisfactory solution, and we have therefore taken a pragmatic stand and chosen a strict concept of *Hapalopilus* as a polypore genus and expanded the genus *Phlebiopsis* to include *Castanoporus*, leaving classification for the rest of the clade unresolved.

Thus defined, *Hapalopilus* is a small genus, currently with four polypore species (Figure 4). The rest of the species currently accepted in *Hapalopilus* (11 species), with different pigmentation and denser fruiting body consistency (cf. *Aurantiporus croceus*), do not belong to Phanerochaetaceae but rather to Meruliaceae (Figure 2) and probably also other families. The expanded concept makes *Phlebiopsis* variable in terms of fruiting body morphology: smooth and effused (*Phlebiopsis*), poroid effused (*Castanoporus*), and stereoid, pileate species with smooth hymenophore (*Hjortstamia*). Microscopically the genus is rather uniform but not distinguishable from *Phaeophlebiopsis*, so for now we have had to abandon a strictly morphological genus concept for this species group.

The genus *Riopa* described by Reid (1969) has been considered a taxonomic synonym of *Ceriporia*, typified by *C. viridans* (Irpicaceae, Figure 2). This conclusion arises from an incorrect interpretation of the identity of the type species of the genus, *R. davidii*, as *Ceriporia camaresiana* (Ryvarden 1991, Bernicchia 2005). Our study of the type specimen shows that *R. davidii* is instead a synonym of *Ceriporia metamorphosa* (=*Riopa metamorphosa*, Phanerochaetaceae). The species called *Ceriporia davidii* (=*Riopa davidii*) by Pieri and Rivoire (1997) turns out to be an undescribed member of the *Ceriporia* clade in the Irpicaceae. The new species, named here as *C. pierii*, and four other newly described species form a well-supported group within the *Ceriporia* clade (Figure 2).

Riopa metamorphosa has been placed previously also in the genus *Emmia*, typified by *Emmia latemarginata* (=*Rigidoporus latemarginatus*) (Zmitrovich et al. 2006). That species is a close relative of *Irpex lacteus* (Irpicaceae), and thus *Riopa* and *Emmia*, though morphologically quite similar, are widely separate phylogenetically (Figure 2, Binder et al. 2013, Zmitrovich and Malysheva 2014).

Discussion

In our treatment, Phanerochaetaceae contains 14 genera, half of them with poroid species. We expect further sampling to result in more polypores and polypore genera for the family. Even so, corticioid species and genera will likely dominate Phanerochaetaceae.

Our taxonomic revision has managed to retain morphological genus concepts within Phanerochaetaceae, although this has required creation of three new genera for polypores. We show that natural genera (*Phanerochaete*, *Phlebiopsis*) contain a wide

variety of hymenophore types — poroid, hydnoid and smooth — and can be best defined with a combination of microscopic characters of fruiting bodies. However, in one case (the *Phlebiopsis* clade, genus *Rhizochaete* in particular) no morphologically unique, phylogenetically justified genera could be defined, and we have felt the need to adopt an interim, partial classification arrangement.

Our results mirror those of Miettinen et al. (2012), whose similar treatment of Steccherinaceae identified genera (*Antrodiella*, *Metuloidea*, *Steccherinum*) each with variable hymenophore types (poroid, hydnoid or smooth). Like us, they found it generally possible to integrate phylogenetic information and morphological genera, but also identified one clade (*Steccherinum*), for which no morphologically satisfactory genus arrangement was in reach.

These studies reinforce the view that genera of macrofungi may contain species with widely variable fruiting body morphology. It seems that morphological genus concepts do have a future, but in many cases only when based on a wide set of microscopic characters. Finally, in a small minority of cases, it appears that morphologically unique genera of macrofungi may not be feasible.

Any taxonomist working with DNA sequences has the advantage of comparing their taxa with publically available sequences regardless of morphology of the source. We encourage a broad-minded approach outside traditional morphological conventions in taxonomic studies. When studying genus limits in particular, sampling and taxonomic treatment should be extended to include all the taxa with similar micro-morphology and DNA sequences.

What factors gave rise to the diversity of fruiting body types in Phanerochaetaceae? We believe that ecological specialization is the major factor in driving fruiting body evolution within the family. For instance, rhizomorphic species with pellicular, simple fruiting bodies in *Phanerochaete* and *Rhizochaete* prefer decaying wood in advanced stages of decomposition and seem to colonize suitable substrates by growing through soil vegetatively. Their closest relatives in *Phanerochaete* and *Phlebiopsis* with denser fruiting bodies occur more frequently on recently fallen logs or even still attached branches. Most poroid, hydnoid and stereoid Phanerochaetaceae with relatively complex fruiting bodies produce them in earlier stages of wood decomposition, living trees or drier microclimatic conditions (*Bjerkandera*, *Donkia*, *Oxychaete*, *Phlebiopsis castanea*, *Pirex*, *Porostereum*, *Riopa metamorphosa*, *Terana*).

We see here a pattern where simple, ephemeral, rhizomorphic fruiting bodies belong mainly to species growing in soil and very decayed wood, whereas more persistent, complex and denser fruiting bodies tend to belong to species inhabiting living or recently dead trees. Species specialized in colonizing quickly consumed substrates such as rotten pieces of wood in soil are probably better off producing short-lived, simple fruiting bodies. Species using more concentrated and longer-term energy sources, such as recently fallen logs, can invest in more complex or longer-living fruiting bodies. Yet Phanerochaetaceae includes no species with long-lived perennial fruiting bodies, and it might be that the genetic make-up of species in the family sets limits to evolution of fruiting body forms.

Taxonomy

Castanoporus Ryvarden

Synopsis Fungorum 5: 121 (1991).

Type species. *Castanoporus castaneus* (Lloyd) Ryvarden

Remarks. This monotypic genus contains one conifer-dwelling resupinate polypore species from East Asia. With its simple-septate hyphae, monomitic and dense structure (in basal layer) with thick-walled hyphae, middle-sized spores and subulate, encrusted cystidia the species brings into mind *Phlebiopsis* under the microscope. For a more detailed description see Nuñez and Ryvarden (2000).

Phylogenetically the species comes close to *Phlebiopsis flavidoalba* and *P. pilatii*. Together those three species form a sister clade to core *Phlebiopsis*, typified by *P. gigantea* (Figures 2 and 3). For now the most practical solution is to include *Castanoporus* in *Phlebiopsis* (see discussion under *Phlebiopsis*). Hjortstam (1987) listed *Castanoporus castaneus* under *Phlebiopsis* in his check-list of corticioid fungi, but made no formal combination. If *Phlebiopsis* would be defined more strictly, then *Castanoporus* could be put in use.

The genus *Cystidiophorus* has been described for *Castanoporus castaneus*, but for nomenclatural reasons described below we think *Castanoporus* should prevail against *Cystidiophorus*. Bondartsev and Ljubarsky (1963) described the monotypic genus *Cystidiophorus* with the species *C. merulioideus* as the type. Unfortunately, they did not indicate a type specimen for the species, which makes the species name invalid, and also rendered the genus invalid (Melbourne Code Art. 40; the cut-off year for type indication is 1958). Later, Imazeki (Imazeki and Hongo 1965) made the combination *Cystidiophorus castaneus* based on *Merulius castaneus* Lloyd, mentioning *C. castaneus* and *C. merulioideus* as synonyms. This combination does not qualify as a validation of Bondartsev and Ljubarsky's genus name, because Imazeki did not provide reference to the genus description, which is clearly separate from the species description in the original paper (Art. 38.1). In such a case, the genus could be considered valid with the condition that no previously described species is mentioned (Art. 38.5a), but this is not the case as Imazeki mentions Lloyd's species. Thus, we follow Ryvarden (1991) and regard *Castanoporus* as the correct name for this genus.

Ginns (1969) lectotypified *C. castaneus* and gave a description of the type, which agrees well with our concept of the species as well as that of Imazeki's and Bondartsev's. Also Maas Geesteranus (1974) studied the lectotype from BPI.

Zmitrovich et al. (2006) combined *C. castaneus* in *Australohydnum*. We do not have material of *Australohydnum* from Australia (the type locality of the type species) or any sequences, but judging from the type of cystidia and hyphal structure we think it is unlikely (but possible) that *Australohydnum* belongs to *Phlebiopsis* as delineated here (see *Oxychaete* for further notes on *Australohydnum*). If *Phlebiopsis* were to be split, *Castanoporus* and *Australohydnum* would probably both persist being morphologically quite distinct.

Hapalopilus P. Karst.

Revue Mycologique Toulouse 3(9): 18 (1881).

Type species. *Hapalopilus nidulans* (Fr.) P. Karst. (= *H. rutilans* (Pers.) Murrill)

Description. Pileate to resupinate polypores with soft to cottony corky, ochre to pink basidiocarps. Hyphal structure monomitic, clamps always present, generative hyphae slightly thick-walled, 2–5.5 µm in diameter, CB–, IKI–, KOH–, covered with granular, golden yellow pigment that dissolves in KOH turning purple. Cystidia absent. Hymenial cells relatively long, 12–25×4.2–5.5 µm. Spores ellipsoid to subcylindrical, thin-walled, 3–5×2–3.2 µm.

Remarks. Altogether 36 species have been combined to *Hapalopilus*, most of them bright-colored, soft polypores with a monomitic, clamped hyphal system. The genus type *H. nidulans* belongs to the Phanerochaetaceae as shown by us (Figure 2) and previous work (Binder et al. 2005, Binder et al. 2013, Floudas and Hibbett 2015). Other species traditionally referred to this genus (*H. alborubescens*, *H. croceus*, *H. ochraceolateritius* etc.) belong to other lineages of the *Polyporales* (Niemelä et al. 2012, Dvořák et al. 2014), and their phylogeny and taxonomy will be revisited on further occasion.

Here we include four species in *Hapalopilus* in the strict sense, three of which are new to the genus. According to our data, *Hapalopilus rutilans* is a holarctic species, *H. eupatorii* and *H. ribicola* are found in Europe, and *H. percoctus* is so far only known from the type locality in Botswana. These species are morphologically very similar, and thus *Hapalopilus* as a genus is morphologically easy to characterize. The purple KOH reaction of *Hapalopilus* is shared by its pigmented, corticioid relatives in *Rhizochaete* (Wu et al. 2010, Chikowski et al. 2016).

Unlike other Phanerochaetaceae polypore genera recognized here, *Hapalopilus* has a typical polypore subhymenium of sinuous, tightly packed, interwoven hyphae instead of the loose corymb type seen in *Oxychaete*, *Phanerina*, *Phanerochaete* and *Riopa*. Also *Phlebiopsis* species (including *Castanoporus*) have an interwoven subhymenium.

Morphological, ecological and geographic data of *Hapalopilus* species are summarized in Table 3.

Hapalopilus eupatorii (P. Karst.) Spirin & Miettinen, comb. nov.

MycoBank 817920

Figures 5b and 6e

≡*Physisporus eupatorii* P. Karst., Revue Mycol. 6: 214 (1884).

=*Ceriporiopsis herbicola* Fortey & Ryvarden.

Remarks. *H. eupatorii* has completely resupinate, thin basidiocarps on dead herbaceous stems (*Arctium*, *Eupatorium*, and *Reynoutria*). It has been recorded once on thin fallen branches of *Robinia* in a thicket of *Reynoutria*. Karsten (1884) described the species from

Table 3. Comparison of *Hapalopilus* species. Spore statistics of *H. rutilans* include only European specimens.

Species	Distribution	Hosts	Basidiocarp	Pores per mm	Tramal hyphae diameter	Basidiospores
H. eupatorii	temperate Europe	dead herbaceous stems, one record on *Robinia*	effused, small-sized	2–4	2.0–3.2(4.2) µm, median=3.0 µm, n=30/1	ellipsoid, (3.3)3.4–4.5(5.2)×(2.2)2.4–3.1(3.2) µm, L=3.96 µm, W=2.75 µm, Q=1.44, n=91/2
H. percoctus	Botswana	dicot log, savanna/park	pileate, projecting several cm	3–4	(2.0)3.0–4.8(5.6) µm, median=4.3 µm, n=21/1	ellipsoid, (3.7)3.8–4.6×(2.7)2.8–3.3 µm, L=4.11 µm, W=2.98 µm, Q=1.38, n=30
H. ribicola	North Europe	dead, still attached branches of *Ribes*	effused-reflexed or resupinate, pilei poorly developed, projecting up to 0.5 cm	3–4	3.0–4.0(4.3) µm, median=3.7 µm, n=30/2	narrowly ellipsoid to ellipsoid, (3.9)4.0–5.0(5.2)×(2.2)2.3–3.0(3.3) µm, L=4.36 µm, W=2.66 µm, Q=1.64, n=90/3
H. rutilans	holarctic	twigs and logs of deciduous trees, rarely also conifers	sessile or effused reflexed, pilei projecting up to 1–5 cm	3–4	(2.0)3.0–3.7(4.6) µm, median=3.3 µm, n=121/8	cylindrical to narrowly ellipsoid, (3.1)3.2–5.1(5.8)×(1.9)2.0–2.7(3.1) µm, L=4 µm, W=2.3 µm, Q=1.74, n=400/13

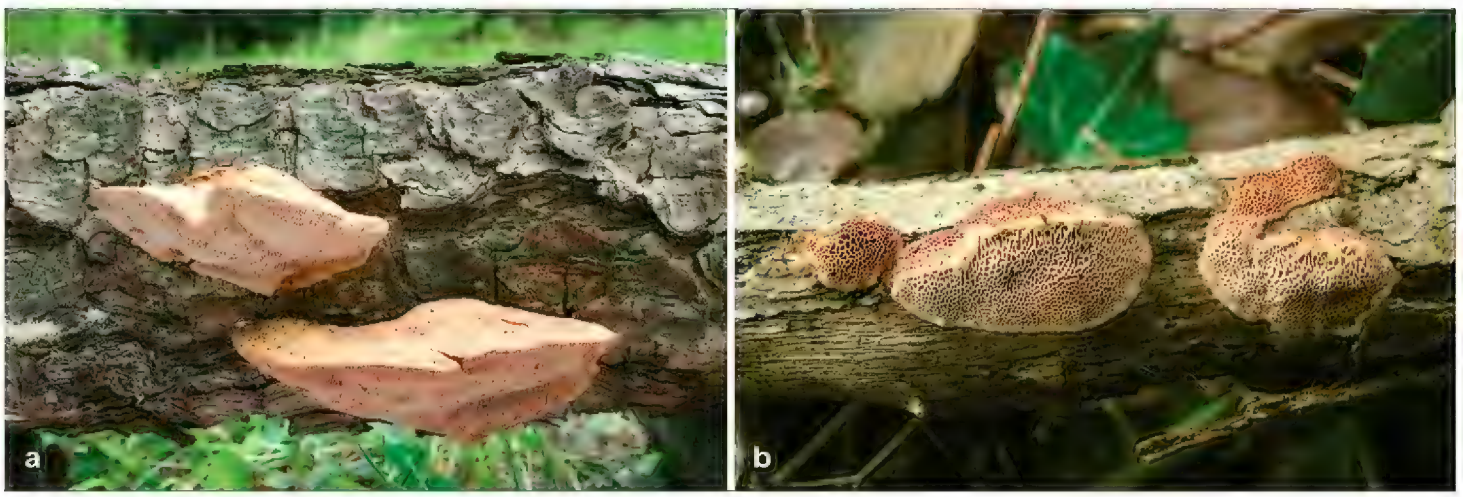

Figure 5. *Hapalopilus* fruiting bodies, **a** *Hapalopilus rutilans*, Vlasák Jr. 0407/34-J **b** *Hapalopilus eupatorii*, Rivoire 5333.

France as *Physisporus eupatorii*, but it long remained an enigma for mycologists (Lowe 1956, Donk 1974). Recently it was reported from England as *Ceriporiopsis herbicola* (Fortey and Ryvarden 2007) and Germany as *H. nidulans* f. *resupinata* (Dämmrich 2014).

***Hapalopilus percoctus* Miettinen, sp. nov.**
MycoBank 817921
Figure 6

Holotype. Botswana. Gaborone, Golf course, -24.652°: 25.936°, strip of natural bush, felled log or tree stump (40 cm in diameter), 28 May 2008, Reijo Miettinen (H 7008581).

Etymology. *Percoctus*, parched, scorched; refers to the sun-exposed habitat of the species.

Remarks. Similar to *Hapalopilus rutilans* with pileate basidiocarps. Microscopically otherwise identical, but *H. percoctus* has clearly wider spores and tramal hyphae (Table 3). The spore dimensions come close to *H. eupatorii*, which has larger pores, effused basidiocarps and grows usually on woody herbs. Its tramal hyphae are also narrower. *Hapalopilus percoctus* is the only species in the genus known to us from the Southern Hemisphere.

***Hapalopilus ribicola* (P. Karst.) Spirin & Miettinen, comb. nov.**
MycoBank 817922
Figure 6g

≡*Trametes ribicola* P. Karst., Hedwigia 20: 178 (1881).

Remarks. This species was described by Karsten (1881) based on the sole collection from Finland. It had usually been regarded as a form of *H. rutilans* (Lowe 1956). However, our data show that specimens growing on *Ribes* spp. in North Europe are

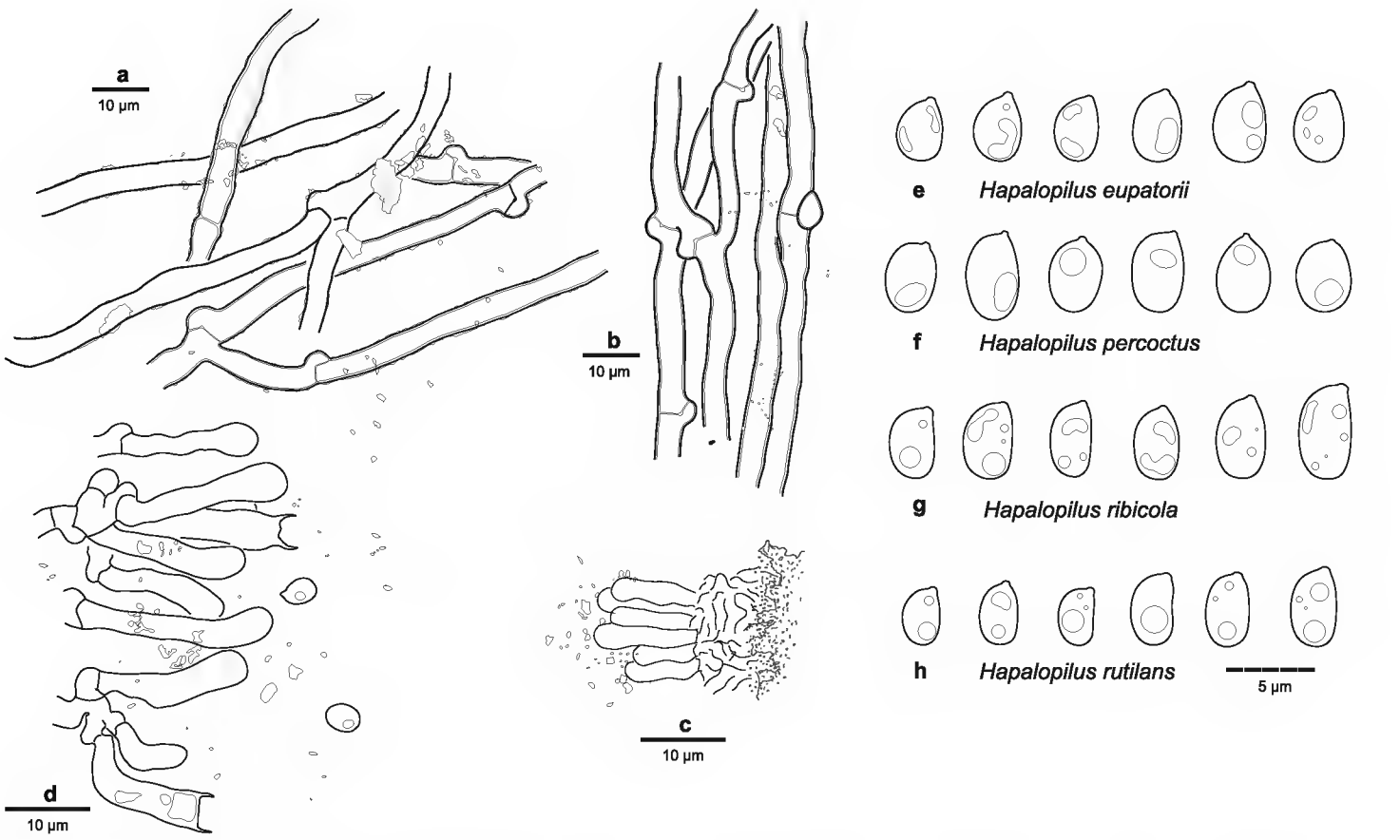

Figure 6. Microscopic characters of *Hapalopilus*. *Hapalopilus percoctus*, holotype, **a** subicular hyphae **b** tramal hyphae **c** hymenium and subhymenium **d** hymenial cells. Spores of **e** *Hapalopilus eupatorii*, lectotype **f** *Hapalopilus percoctus*, holotype **g** *Hapalopilus ribicola*, lectotype **h** *Hapalopilus rutilans*, Niemelä 7134.

distinct from *H. rutilans* and phylogenetically closer to *H. eupatorii*. All specimens of *H. ribicola* studied by us are from Finland, from branches of both wild and cultivated *Ribes* spp. The species is evidently widely distributed and just overlooked.

Hapalopilus rutilans **(Pers.) Murrill**

Figures 5a and 6h

≡*Boletus rutilans* Pers., Icones et Descriptiones Fungorum Minus Cognitorum 1: 19, t. 6:3 (1798).
=*Hapalopilus nidulans* (Fr.) P. Karst.

Remarks. This common species has gone under two names, *H. rutilans* and *H. nidulans*. Many authors have chosen to use *H. nidulans* over *H. rutilans*, (Bondartsev 1953, Gilbertson and Ryvarden 1986, Bernicchia 2005, Ryvarden and Melo 2014), but also the latter name has been in use (Murrill 1904, Donk 1974, Niemelä 2005). *Hapalopilus rutilans* is an older name than *H. nidulans*, and since both were sanctioned by Fries, the former has priority (ICBN Melbourne code art. 15.4).

Neither of the names has been typified. Persoon's original publication includes a rather uninformative painting of the fungus, probably *Hapalopilus rutilans* or *Inonotus*

sensu lato. The original description of *H. nidulans* is similarly scanty. No material suitable for lectotypification remains of either species, so we have chosen to designate neotypes for both species to fix the nomenclature: *H. rutilans* based on a French specimen from oak in accordance to the protologue (Persoon 1798) as Persoon got material mainly from Germany and France, and *H. nidulans* based on a Finnish specimen, since Fries (1821) based his description on his own collection from neighboring Sweden.

Ryvarden (1991) attempted to designate a lectotype for *H. nidulans*. We dispute his typification, since he used an illustration in Bulliard's publication from 1791 as the type, whereas Fries's original work does not refer to Bulliard. The fact that Fries later (1836-1838) referred to Bulliard doesn't make the drawing available for lectotypification: only the original material is valid under the code (ICBN Melbourne art. 9.2, 9.12).

***Oxychaete* Miettinen, gen. nov.**
MycoBank 811534

Type species. *Oxychaete cervinogilva* (Jungh.) Miettinen

Etymology. Constructed from *Oxyporus* and *Phanerochaete*, but can be interpreted as "bearing sharp setae".

Description. Effused-reflexed polypores with yellow-brown colors, light cardboard-like consistency and large, shallow pores. Monomitic, simple-septate, with slightly thick-walled hyphae and abundant subulate, naked, thick-walled cystidia of subhymenial origin. Hymenial branching corymb-like. Spores curved cylindrical, large (6–8×3–3.5 μm).

Remarks. Other hydnoid and poroid genera with simple-septate hyphae and encrusted, thick-walled cystidia include *Australohydnum*, *Phlebiopsis*, *Flavodon* and *Irpex*. The latter two are phylogenetically distantly related to *Oxychaete*, and they possess dimitic hyphal structure quite different from the loose monomitic structure of *Oxychaete*. *Phlebiopsis* is phylogenetically distinct from *Oxychaete* (Figure 2), and its hyphal structure is more compact, even agglutinated (basal layer). Hyphae are also winding and covered with abundant brownish encrustation, which is lacking in *Oxychaete*. Cystidia are tramal in origin (as opposed to hymenial in *Oxychaete*). Due to the hyphal structure the basidiocarp is tougher and not board-like when cut as in *Oxychaete*.

Australohydnum is a more difficult case to decide on since there are no good references on the microscopic characters of the type species, *Hydnum griseofuscescens* Reichardt from Australia. Descriptions vary so much that it is possible that many species and even genera have been recognized as *Australohydnum dregeanum* (Berk.) Hjortstam & Ryvarden and its supposed synonyms (Jülich 1978, Hjortstam and Ryvarden 1989, Gilbertson and Adaskaveg 1993, Melo and Hjortstam 2002, Zmitrovich et al. 2006). Sometimes the structure is monomitic, sometimes dimitic; cystidia may be subulate or obtuse; basidiocarps may be resupinate with smooth hymenophore or hydnoid with caps.

Reid (1955, 1963) refers directly to Australian material and the type, and provides an illustration (under *Irpex vellereus*). His *A. griseofuscescens* is a pileate, hydnoid species with violaceous brownish basidiocarps, very thick-walled, simple-septate hyphae 4–9 μm

in diameter, and abundant long, obtuse, poorly differentiated cystidia with tramal origin and fine apical encrustation. Reid states that the hyphal structure is monomitic, but has also drawn long aseptate hyphae. Spores are ellipsoid, medium-sized. The description and illustrations provided by Melo and Hjortstam (2002) from Portugal are very similar to those of Reid, and agree largely with an Indian specimen we have studied.

Morphology suggests that *A. griseofuscescens* is not congeneric with *Oxychaete cervinogilva*, the latter being a polypore with regular pores, much looser hyphal structure without wide-spread encrustation, more regular and less-thick-walled hyphae, different type of cystidia with hymenial origin, differently shaped spores and lighter color of the basidiocarp.

***Oxychaete cervinogilva* (Jungh.) Miettinen, comb. nov.**
MycoBank 811535
Figure 7

≡*Polyporus cervinogilvus* Jungh., Praemissa in floram cryptogamicam Javae insulae: 45 (1838).

Description. Basidiocarp half-resupinate to pileate, annual, upper surface felt-like, yellowish brown with a lighter margin, lower surface brownish yellow or light ochraceous, 1–2 mm thick, caps projecting up to 3 cm, can fuse to form wide fruiting bodies. Consistency light cardboard-like when dry, somewhat flexible but easy to break apart. Pores regular, thin-walled, mouths rather smooth, (1)2–3 per mm. Cap context and subiculum yellowish brown, homogenous, upper surface not differentiated, up to 1 mm thick. Cap with a sharp, 1 mm wide sterile margin.

Hyphal system monomitic, clamps absent. Hyphae homogenous throughout, mostly thick-walled, always with a wide lumen, rather stiff and straight, CB– to CB(+), IKI–, KOH–, CRB lilac. Encrustation absent except on cystidia. Subicular hyphae interwoven, loosely arranged, (3.2)4–5.4(7.5) µm in diameter, walls up to 1.5 µm thick, mostly ≤1 µm. Contextual hyphae mostly horizontally arranged but not strictly parallel, (3.8)4–5.1(5.5) µm in diameter. Tramal tissue loose and easy to study, hyphae rather straight, parallel in lower trama, subparallel and interwoven towards subiculum, (3)3.5–4.8(6.2) µm in diameter, walls mostly 0.8–1.2 µm thick. Subhymenial hyphae thin- to slightly thick-walled, richly branching mostly like a corymb, not much winding.

Cystidia abundant, hymenial, thick-walled, often with an apical crystal cap, (15)20–40(55)×4.5–9, projecting 5–25 µm above hymenium.

Hymenium dominated by basidioles and cystidia, cells with constrictions especially in older basidiocarps. Basidia cylindrical to narrowly clavate, collapsing upon spore release and difficult to spot, with 4 sterigmata. Cystidioles absent.

Basidiospores cylindrical, curved, thin-walled, smooth, (5.9)6–8.4(8.9)×2.8–3.7(3.8) µm, L=6.93 µm, W=3.17 µm, Q'=(1.8)1.9–2.5(2.6), Q=2.19, CB–, IKI–, plasma stains in CB.

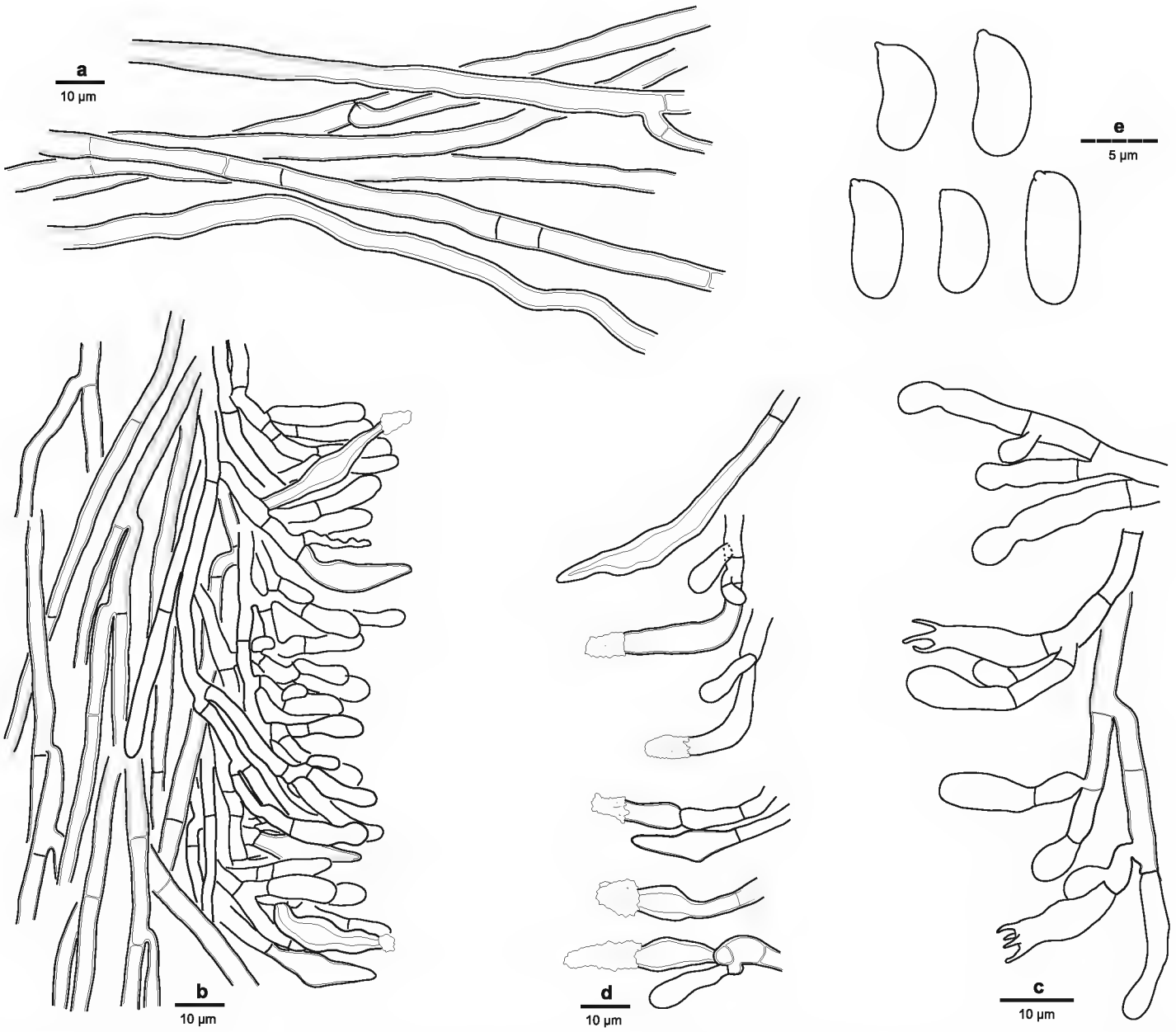

Figure 7. Microscopic characters of *Oxychaete cervinogilvus*, Schigel 5216, **a** subicular hyphae **b** tube trama and hymenium **c** hymenial cells **d** hymenial cystidia **e** spores.

Distribution. Tropical Asia and Australia (Ryvarden and Johansen 1980). Not common in Indonesia although described from there.

Ecology. Apparently prefers small-diameter dead wood of angiosperms. According to the description, the type was collected in a wet, shady forest in Javanese mountains. Australian collections we have seen are from drier localities (monsoon forest and city park).

Remarks. Junghuhn (1838) provides a good painting of the species (Tab. IX), available through Google books (https://books.google.fi/books?id=AFJUAAAAcAAJ).

***Phanerina* Miettinen, gen. nov.**
MycoBank 811536

Type species. *Phanerina mellea* (Berk. & Broome) Miettinen.

Description. Basidiocarps resupinate, yellow, fragile, pores shallow and large (1–4 per mm). Hyphal structure monomitic, simple-septate, loose, hyphae not swollen, wider (4–5 µm in diameter) in subiculum, a bit narrower in trama (3–4 µm). Hymenial branching corymb-like, subulate thin-walled cystidia present. Spores rather large (6–7×3 µm), cylindrical to narrowly ellipsoid.

Remarks. This monotypic genus comes close to *Riopa* both morphologically and phylogenetically, though the two do not seem to form a monophyletic group (Figure 2). Morphological differences are summarized in Table 2.

***Phanerina mellea* (Berk. & Broome) Miettinen, comb. nov.**
MycoBank 811537
Figures 1b and 8

≡*Polyporus melleus* Berk. & Broome, J. Linn. Soc., Bot. 14: 53 (1873).

Description. Basidiocarp resupinate, yellow, ranging from yellowish cream to brownish yellow, 1–10×1–5 cm patches, 1(2) mm thick. Consistency fragile when dry. Pores shallow, somewhat irregular, splitting and eventually may turn dentate, 2–4 per mm, larger when split. Subiculum cream-colored, a bit lighter than pore surface, pellicular, cottony under the lens, 0.1–0.3 mm. Margin thinning out, smooth areas of several millimeters similar to tube bottoms may be present.

Hyphal system monomitic, clamps absent. Hyphae cylindrical, not much swollen, branching in sharp angles, rather similar throughout the basidiocarp, CB– to CB(+), IKI–, KOH–, CRB lilac. Large crystal clumps mostly of rhomboidal shape present in trama. Subiculum loose, hyphae interwoven, slightly thick-walled to thick-walled when old, (2)3–5(6.4) µm in diameter, walls mostly <0.5 µm thick, up to 1.2 µm in old basidiocarps. Tramal hyphae subparallel, thin- to slightly thick-walled, (2)3–3.8(4.8) µm in diameter. Subhymenium branching corymb-like, cells not sinuous, relatively easy to study.

Cystidia present but often rare, hymenial, thin-walled, subulate, rarely septate, naked, 40–80×5.8–9.2 µm, projecting 20–50 µm.

Hymenium relatively loose. Basidia clavate, 15–26×5.2–6.8 µm, with 4 wide, spindle-shaped sterigmata, 4–4.8×1.8 µm.

Basidiospores cylindrical to narrowly ellipsoid, usually abundant, with thin but distinct walls, smooth, (5.2)5.8–7.5(7.8)×(2.8)2.9–3.8(4.4) µm, L=6.55 µm, W=3.26 µm, Q'= (1.6)1.8–2.3(2.4), Q=2.01. Spore shape variation is rather large and abnormally broad ellipsoid spores can be present.

Distribution. Described from Sri Lanka. We can confirm it from East Africa (Tanzania, Kenya), Japan (Okinawa), and Indonesia (New Guinea). Sequences of Chinese specimens are also available in the INSDC.

Ecology. Grows on dead dicot trees, both standing and fallen, often in sun-exposed habitats.

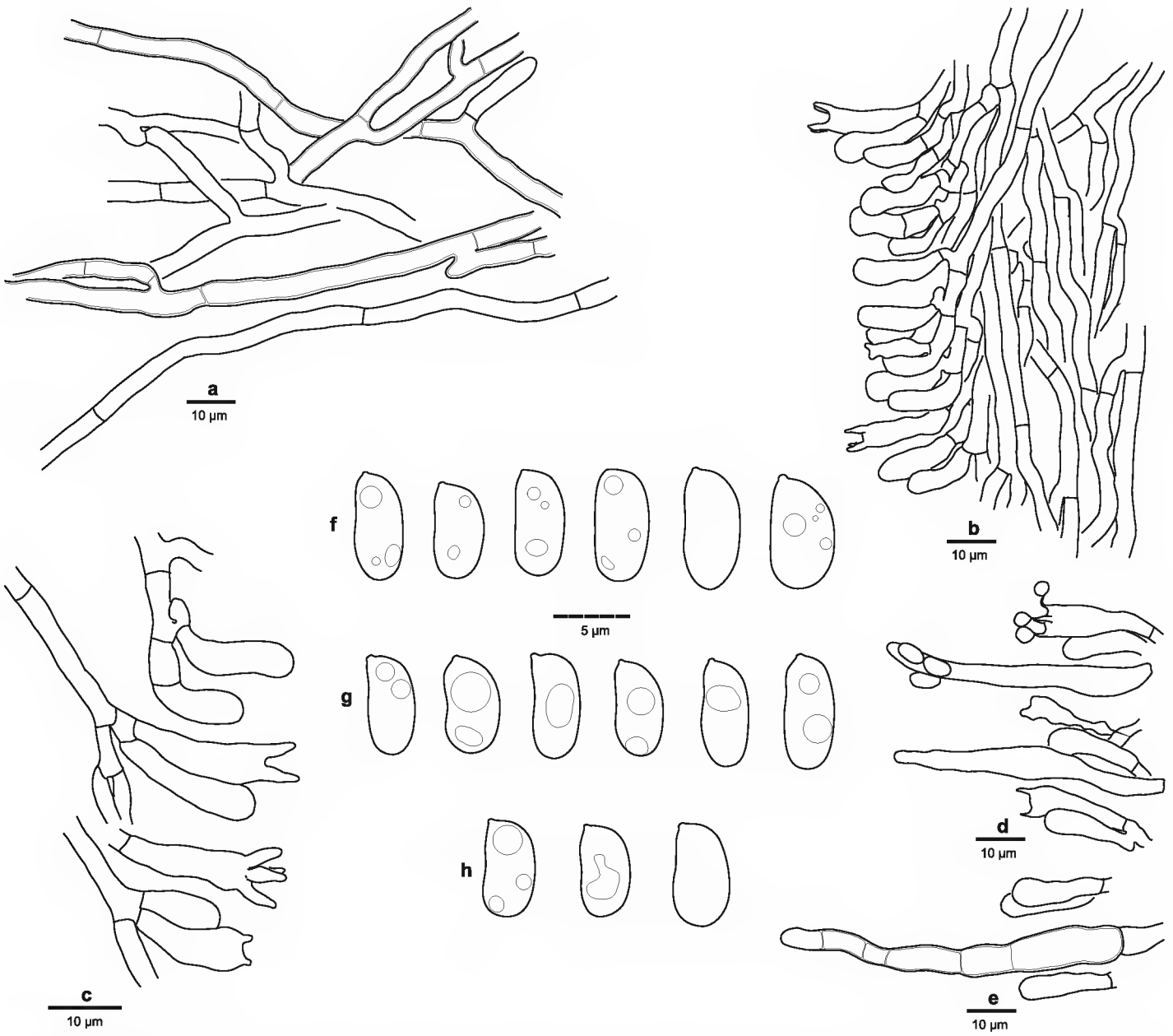

Figure 8. Microscopic characters of *Phanerina mellea*. **a** Subicular hyphae **b** tube trama **c** basidia, Miettinen 9134. Hymenial cystidia **d** Nuñez 503 **e** Ryvarden 10132. Spores **f** lectotype **g** Miettinen 9134 **h** Nuñez 503.

Remarks. East Asian, East African and New Guinean specimens have neither ITS sequence differences nor morphological differences, so we feel it is safe to assume that the type from Sri Lanka belongs to the same species. Morphologically the type specimen agrees very well with other material. Its spores are a little larger on average than in other specimens studied, but considering the large variability in size and shape of spores this is best interpreted as normal variance within species.

Phanerochaete P. Karst.

Bidrag till Kännedom av Finlands Natur och Folk 48: 426 (1889).

Type species. *Phanerochaete alnea* (Fr.) P. Karst.

Phanerochaete inflata **(B.S. Jia & B.K. Cui) Miettinen, comb. nov.**
MycoBank 818689

≡*Ceriporia inflata* B.S. Jia & B.K. Cui, Mycotaxon 121: 306 (2012).

Remarks. We have chosen to apply the genus name *Phanerochaete* for most of the *Phanerochaete* clade, excluding the three polypore genera *Oxychaete*, *Phanerina* and *Riopa* (Figure 2). Morphologically, species in the *Phanerochaete* clade share microscopic characters such as simple-septate, relatively simple, loose hyphal structure, mid-sized hymenial cells, mid-sized straight cylindrical to narrow ellipsoid spores, and cystidia of subhymenial origin (Table 1 and 2). However, cystidia are rare and poorly differentiated or absent in three of the polypores (in the genera *Phanerina* and *Riopa*), and spores are distinctly curved in two species (*Riopa*). The third newly introduced polypore genus *Oxychaete* with its encrusted cystidia and large spores produces pileate and poroid basidiocarps. With the inclusion of these species, the genus *Phanerochaete* would become difficult to define morphologically.

Ceriporia inflata described by Jia and Cui (2012) belongs to Phanerochaetaceae with *P. raduloides* as the closest relative (Figure 2). The hymenophore of *C. inflata* is composed of irregular pores with lacerate mouths, and that of *P. raduloides* of irregular teeth. Also *Ceriporia jianxiensis* (no sequence available) described in the same paper as *Ceriporia inflata* may be closely related. Their identity against *P. capitata* and *P. aculeata* along with other species in the *P. raduloides* group should be checked.

For now we consider *Ceriporia inflata* a species of *Phanerochaete*. Splitting the hydnoid-poroid *Phanerochaete* of this group into a separate genus (possibly *Phanerodontia* Hjortstam) would make it necessary to split *Phanerochaete* into many small genera and would place morphologically very similar corticioid species into separate genera. For this reason we strongly prefer a wide concept of *Phanerochaete* that includes the hydnoid and poroid members, which are microscopically very similar to *Phanerochaete* sensu typi. See Tables 1 and 2 for characterization of the genus against similar genera in the Phanerochaetaceae.

Hjortstam and Ryvarden (2010) described *Phanericium* and *Phanerodontia* for a few species placed traditionally in *Phanerochaete*. Their *Phanerodontia* includes four taxa with smooth to hydnoid hymenophores. *Phanerodontia* is probably a taxonomic synonym of *Phanerochaete*. Although the type, *P. dentata*, has not been sequenced, two other members of the genus have (*P. chrysosporium* and *P. magnoliae*). They clearly belong to *Phanerochaete*, and according to the *rpb1* dataset to the same subclade within the genus with smooth to poroid members (Figure 3). *Phanerodontia dentata* does not closely resemble any polypore genus discussed here (except *Phanerochaete*) with its combination of thin-walled tubular cystidia, long basidia, thick-walled subicular hyphae and ellipsoid spores.

Phanericium is a monotypic genus, and the type *P. subquercinum* is characterized by hydnoid, effused fruiting bodies, absence of cystidia, hyphae of even width throughout the fruiting body and broad ellipsoid spores. This set of characters does not closely match taxa discussed in detail in this paper, and more detailed study is needed to conclude whether the genus belongs to Phaerochaetaceae.

***Phlebiopsis* Jülich**

Persoonia 10: 137 (1978).

Type species. *Phlebiopsis gigantea* (Fr.) Jülich.

***Phlebiopsis brunneocystidiata* (Sheng H. Wu) Miettinen, comb. nov.**
MycoBank 817923

≡*Phanerochaete brunneocystidiata* Sheng H. Wu, Mycotaxon 90: 423 (2004)

***Phlebiopsis castanea* (Lloyd) Miettinen & Spirin, comb. nov.**
MycoBank 817928

≡*Irpex castaneus* Lloyd, Mycological Writings 6 (65): 1060 (1920)

***Phlebiopsis friesii* (Lév.) Spirin & Miettinen, comb. nov.**
MycoBank 817924

≡*Thelephora friesii* Lév., Systematisches Verzeichnis der im indischen Archipel in den Jahren 1842–1848 gesammelten sowie aus Japan empfangenen Pflanzen (1854)

***Phlebiopsis laxa* (Sheng H. Wu) Miettinen, comb. nov.**
MycoBank 817925

≡*Phanerochaete laxa* Sheng H. Wu, Botanical Bulletin of the Academia Sinica (Taipei) 41: 169 (2000)

***Phlebiopsis papyrina* (Mont.) Miettinen & Spirin, comb. nov.**
MycoBank 817926

≡*Stereum papyrinum* Mont., Annales des Sciences Naturelles Botanique 17: 125 (1842)

***Phlebiopsis pilatii* (Parmasto) Spirin & Miettinen, comb. nov.**
MycoBank 817927

≡*Laeticorticium pilatii* Parmasto, Eesti NSV Teaduste Akadeemia Toimetised 14(2): 228 (1965)

Remarks. *Phlebiopsis* is typified by *P. gigantea*, a phlebioid species with agglutinated lower subiculum, well-developed basal layer/upper subiculum, thick-walled, simple-septate hyphae and thick-walled, conical, encrusted cystidia (lamprocystidia). Our wider concept of *Phlebiopsis* dilutes this set of characters, but lamprocystidia, interwoven subhymenium and tightly built subiculum remain as important characters for genus delimitation against similar genera of the Phanerochaetaceae (Table 1).

Hjortstamia crassa has been shown to be a close relative of *Phlebiopsis*, and has been included in that genus (Floudas and Hibbett 2015). We agree with this conclusion. The type species of *Hjortstamia* (*H. friesii*) has not been sequenced, but it is very similar to *H. crassa*. Thus *Hjortstamia* should for now be considered as a taxonomic synonym of *Phlebiopsis*. In addition to the above-mentioned *Hjortstamia* spp., a third similar species, *H. papyrina*, is combined to *Phlebiopsis* on morphological grounds.

The two main differences that have been emphasized to separate *Hjortstamia* from *Phlebiopsis* are reflexed basidiocarps and the loose subiculum of the former as opposed to the dense, agglutinated subiculum and totally effused basidiocarps of the latter. A closer look reveals that the difference is not as striking as often described. Whereas the genus type of *Hjortstamia* — *H. friesii* — and its close relative *H. papyrina* are distinctly pileate, basidiocarps of *Hjortstamia crassa* are much of the time fully resupinate or caps are small. *Hjortstamia crassa* also has an agglutinated upper subiculum or basal layer similar to agglutinated *Phlebiopsis* structures, as depicted by Wu and Chen (1992). *Hjortstamia friesii* has a tight (though not agglutinated) subicular layer composed of parallel hyphae as well (Hjortstam and Ryvarden 1989, Boidin and Gilles 2002). Subicular/cystidial hyphae of the above-mentioned species are strikingly similar, thick-walled, straight, stiff and sparsely septate.

A loose subiculum or pileate fruiting bodies do not seem to be useful characters separating *Hjortstamia* from *Phlebiopsis*, since loose and agglutinated species are widely intermixed phylogenetically within *Phlebiopsis* sensu lato (Figure 2). *Hjortstamia crassa* for instance is more closely related to the type species of *Phlebiopsis* than is *Phlebiopsis flavidoalba* with a very dense structure and effused fruiting bodies.

Sequences made available by Wu et al. (2010) include *Phanerochaete brunneocystidiata* and *Phanerochaete laxa*. The former is based on a paratype and the latter on the holotype. Wu combined the species in *Hjortstamia* due to sequence similarity to *H. crassa*. We haven't seen authentic material, but according to original descriptions, they seem to share basic *Phlebiopsis* characters except that no agglutinated layer was described (Wu 2000, 2004).

Some *Phlebiopsis* species may turn out to belong to the *Hapalopilus-Rhizochaete* subclade instead of the *Phlebiopsis* subclade. For instance *Phlebiopsis roumeguerei* is nested within *Phaeophlebiopsis* as defined by Floudas and Hibbett (2015). More in-depth research is needed to settle genus classification for *Rhizochaete* and *Phaeophlebiopsis*-like taxa.

Riopa D. A. Reid

Revue Mycol., Paris 33: 244 (1969).

Type species. *Riopa davidii* D. A. Reid (=*Riopa metamorphosa* (Fuckel) Miettinen & Spirin).

Description. White, resupinate polypores with shallow pores, 2–5 per mm. Hyphal structure monomitic, clamps absent. Hyphae thin- to slightly thick-walled, similar throughout the basidiocarp, hyphae not swollen, wider (3–5 µm in diameter) in subiculum, a bit narrower in trama (2.8–3.5 µm). Hymenial branching corymb-like. Thin-walled, poorly differentiated hymenial cystidia and conidia in one species. Spores curved cylindrical, sausage-like, thin-walled, mid-sized (4.5–6.5×2–3 µm).

Remarks. Reid (1969) described *Riopa* as a monotypic genus with *Riopa davidii* D. A. Reid from Corsica as the sole species. Ryvarden (1991) considered *R. davidii* as a synonym of *Ceriporia camaresiana* (Bourdot & Galzin) Bondartsev & Singer, in effect making *Riopa* a synonym of *Ceriporia*. Pieri and Rivoire (1997) regarded *Riopa davidii* and *Ceriporia camaresiana* as separate species, and made the combination *Ceriporia davidii*. Their concept of the species was mixed, as can be seen already from the spore variation they report. Their specimens from mainland France did seem to represent a species of *Ceriporia* separate from *C. camaresiana*, and consequently *Ceriporia davidii* was adopted by Bernicchia (2005) and Ryvarden and Melo (2014).

We studied the type of *Riopa davidii*, and it turned out to be a more recent synonym for *Ceriporia metamorphosa* (Fuckel) Ryvarden & Gilb. After studying the French material of *Ceriporia davidii* collected by B. Rivoire, we could also conclude that *Ceriporia davidii* sensu Pieri and Rivoire (1997) needs to be described with a new name (*Ceriporia pierii*). *Ceriporia pierii* and also *C. camaresiana* belong to the *Ceriporia* clade and are only distantly related to *Riopa* (Figure 2).

Riopa metamorphosa (Fuckel) Miettinen & Spirin, comb. nov.

MycoBank 811538

Figures 1d and 9

≡*Polyporus metamorphosus* Fuckel, Jb. Nassau Ver. Naturk. 27–28: 87 (1874) ['1873–74'].

Lectotype. Germany. Oestrich (Nassau): Mittelheimer Vorderwald, rotten trunk of *Quercus*, "Herbier Fuckel 1894, Herbier Barbey-Boissier", no. 2008 (S F43290, designated here).

Epitype. Czech Republic. Moravia: Lanžhot, Ranšpurk virgin forest, rotten trunk of *Quercus robur*, 5 Oct 1988 Pouzar (PRM871894, designated here, duplicate H 7008579).

Description. Basidiocarp resupinate, white, cream or straw-colored, consistency fragile when dry. Forms patches of a few cm that can fuse to extensive basidiocarps, up to 2(-3) mm thick. Pores rounded angular, soon splitting and then irregular and sinuous, mouths smooth, 2–3(4) per mm, up to 2 mm wide when split. Subiculum very thin, arachnoid to

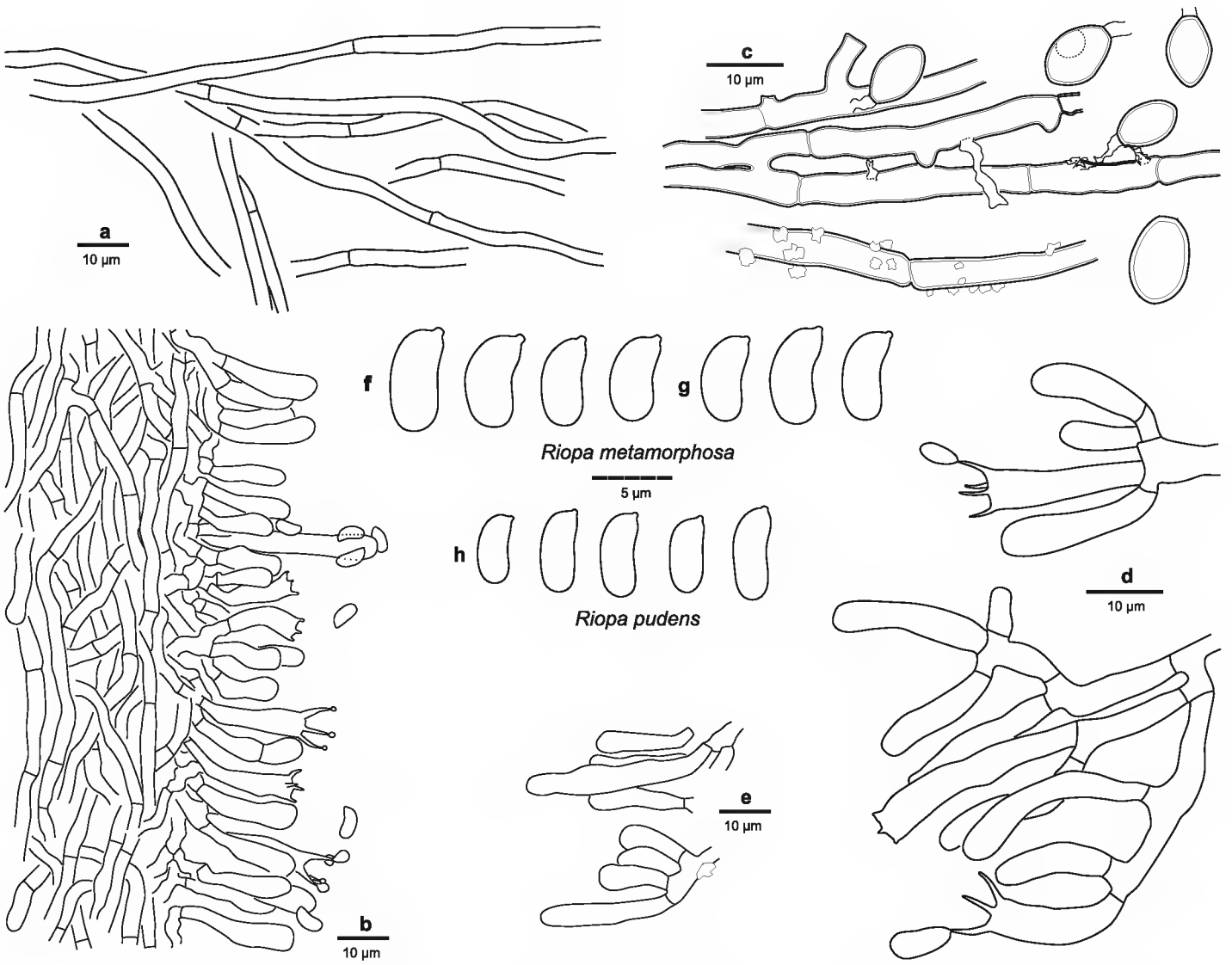

Figure 9. Microscopic characters of *Riopa*. *Riopa metamorphosa*, epitype: **a** subicular hyphae **b** tube trama and hymenium **c** anamorph (*Sporotrichum aurantiacum*) **d** basidioles and basidia showing the characteristic corymb branching **e** hymenial cystidia. Spores of **f** *Riopa metamorphosa* drawn from the holotype of *R. davidii* **g** epitype of *R. metamorphosa* **h** holotype of *R. pudens*.

pellicular, white to cream, often lighter than pores. Margin thinning out, usually no sterile margin.

Hyphal system monomitic, simple septate, hyphae rather homogenous throughout. Subicular hyphae interwoven, tissue loose, hyphae thin-walled to slightly thick-walled, (2.8)3.2–4.4(6.4) µm, walls rarely up to 1 µm in diameter. Tramal hyphae thin- to slightly thick-walled, interwoven but mostly vertically arranged, (2.2)2.9–3.5(4.0) µm in diameter. Subhymenium relatively loose, structure uncharacteristically simple for a polypore, composed of branching corymb-like, straight hyphae similar to those in trama. Crystals present as irregular aggregates of rhomboidal plates of various sizes, also fine encrustation present in subiculum. Shiny, hyaline, amorphous droplets floating around in CB.

Cystidia thin-walled, cylindrical, projecting above hymenial layer 5–20 µm, often covered with spores, (15)20–50×4–6.2 µm, born in subhymenium, poorly differentiated, appear as elongated basidioles, rare.

Hymenium loosely arranged, cells thin-walled. Basidia clavate, often projecting slightly above the rest of the hymenium, 15–28(35)×4–5.5(6.2) µm, with 4 sterigmata.

Basidiospores curved cylindrical, thin-walled, (4.2)5–6.6(8.2)×(2)2.2–3.1(3.5) µm, L=5.69 µm, W=2.59 µm, Q=2.19.

Anamorph known as *Sporotrichum aurantiacum* Link present or absent. Most but not all basidiocarps produce at least conidia in subiculum. When the anamorphic stage is well developed, it appears as an orange mass of conidia similar in shape to *Haplotrichum aureum*, in conjunction with basidiocarps or separately. Microscopically composed of thick-walled, ellipsoid to constricted conidia (8.2–12.2×5.2–7.8 µm, n=36/3) born singly as apical parts of slightly to clearly thick-walled, partly encrusted hyphae, (3.2)3.6–4.5(7.2) µm in diameter, walls ≤1.5 µm. The conidia and hyphae are yellow, the plasma of the conidia stains in CB, and the walls are CB– to CB(+) and slightly dextrinoid. In KOH the conidia stain pinkish red in masses. Wakefield (1952) proved in the lab that the polypore and conidial stages belong to the same organism.

Distribution. Temperate Europe: Germany, Poland, Slovakia, Czech Republic, Russia (Nizhny Novgorod), France (mainland, Corsica) (Vampola and Pouzar 1996, Pieri and Rivoire 1997). Northernmost records from Southern Norway (Ryvarden and Melo 2014) and Stockholm, Sweden (Romell 1926).

Ecology. Grows preferably on rotten oak trunks. We have seen it on *Eucalyptus* and *Salix caprea*, also reported on *Castanea*, *Juglands* and *Malus* (Bourdot and Galzin 1928, Ryvarden and Gilbertson 1993, Pieri and Rivoire 1997).

Remarks. Fuckel's herbarium is in Wiesbaden (WIES), but its material is not available for loan. A duplicate of an original Fuckel specimen in Stockholm is chosen as the lectotype here. It represents an almost completely destroyed anamorphic stage. For practical reasons we also select an epitype from the Czech Republic.

Conidia have been reported from few other members of the Phanerochaetaceae: *Phanerochaete chrysosporium* (Burdsall and Eslyn 1974) and *Hyphodermella rosae* (Rahimlou et al. 2015). *Riopa metamorphosa* conidia are similar to the conidia of these species, particularly *Hyphodermella rosae*.

***Riopa pudens* Miettinen, sp. nov.**
MycoBank 811539
Figure 9h

Holotype. Indonesia. Riau: Indragiri Hulu, Bukit Aluran Babi, -0.838: 102.226, selectively logged forest slope, piece of a dicot log (15 cm in diameter, decay stage 2–4/5), 1 Jul 2004, Miettinen 8772 (ANDA, isotype H 7008582).

Etymology. *Pudens* (adj., L), shy, modest, refers to the scarcity of distinct characters.

Description. Basidiocarp resupinate, annual, cream, young parts white, up to half a meter wide, up to 4 mm thick. Consistency resistant to breaking but not tough. Pores thin-walled, mouths finely dentate, splitting when older, angular, 4–5 mm, 2–3 per mm when split/fused, 0.5–1.2 mm long. Subiculum white, 0.1–0.4 mm thick. Margin thinning out.

Hyphal system monomitic, clamps absent. Hyphae not swollen, rather similar in all parts. Subicular tissue loose, hyphae interwoven, thin- to thick-walled, mostly slightly thick-walled, (2.8)3.4–4.8(6.2) µm in diameter, walls rarely up to 1 µm thick. Tramal hyphae vertical, subparallel to interwoven, only moderately winding, thin-walled or slightly

thick-walled, (2.4)2.8–3.2(4.2) µm in diameter. Shiny hyaline resin droplets floating around, fine-grained crystalline-amorphous substance glued on tramal hyphae in CB.

Cystidia not seen.

Hymenium relatively loosely arranged, basidia very thin-walled, collapsing soon, basidioles 10–14×3–4.2 µm.

Basidiospores curved cylindrical, thin-walled, (4.2)4.3–5.6(6.2)×(1.8)1.9–2.2(2.3) µm, L=5.01 µm, W=2.08 µm, Q=2.41.

Distribution. Southeast Asia. Known from Riau, Sumatra and Fujian, China (the INSDC sequence JX623931, Cui 3238, '*Ceriporia camaresiana*').

Ecology. Grows on fairly rotten angiosperm wood. The type comes from low-land rainforest.

Remarks. The species lacks any distinct characters. Cream-colored basidiocarp with non-inflated hyphae and corymb-subhymenium help to distinguish this species from *Ceriporia* spp. It is similar to *Phanerochaete inflata* and *Ceriporia jianxiensis*, but differs in having long-celled, narrower subicular hyphae (mostly <5 µm in diameter). The relatively small cylindrical curved spores exclude *Oxyporus* spp. and *Emmia* spp. Except for the smaller pores and the lack of cystidia and a conidial stage it is very similar to *Riopa metamorphosa*.

Sporotrichum Link

Magazin der Gesellschaft Naturforschenden Freunde Berlin 3(1): 12 (1809).

Type species. *Sporotrichum aureum* Link (= *Riopa metamorphosa* (Fuckel) Miettinen & Spirin)

Remarks. Hughes (1958) lectotypified the genus with *S. aureum*. The original description of *S. aureum* does not permit accurate identification of the fungus in question, and no type seems to exist (Stalpers 1984). Fries (1932) considered *S. aureum* a synonym of *Trichoderma aurantiacum* Pers. 1796 (=*Sporotrichum aurantiacum* (Pers.) Fr). In his monograph of *Sporotrichum* Stalpers (1984) chose to follow Fries. He also considered *S. aureum* as an anamorphic stage of *Riopa metamorphosa*.

To formally settle the names *Sporotrichum*, *S. aureus* and *S. aurantiacum* we need to designate neotypes for the two species in question. In line with Stalper's interpretation, we designate here the collection Vlasák 0511/15 (H 7008577) as the neotype of *S. aureum* Link, and collection Spirin 2456 (H 7029505) as the neotype of *S. aurantiacum*.

This makes *Sporotrichum* an older name available for *Riopa* under the ICBN Melbourne code article 59.1. However, adoption of *Sporotrichum*, traditionally a very heterogeneous set of anamorphs, for a small genus of polypores would only create confusion. Stalpers (1984) described the genus as a "litterbag" of conidiogenous fungi, and accepted only three species. According to him the teleomorphs of those three species are in separate genera (*Laetiporus*, *Phanerochaete* and *Pycnoporellus*/*Riopa*) that we now know are phylogenetically distinct. Although the type species *Riopa* produces an anamorph, we have seen no conidia in the other species of the genus (*R. pudens*). In this

situation it is better to coin *Riopa*, a name without identity problems, for this polypore genus. We suggest conservation of the teleomorphic name *Riopa* D. A. Reid 1968 over the anamorphic *Sporotrichum* Link 1809.

Key to genera of Phanerochaetaceae

1	Hyphae always with clamps	**2**
–	Hyphae mostly with simple septa	**11**
2	Hymenophore with regular pores	**3**
–	Hymenophore smooth, hydnoid or dentate	**4**
3	Basidiocarps ochre yellow in color throughout, with abundant granular, golden pigment when under microscope, purple in KOH	***Hapalopilus***
–	Basidiocarps whitish to grey, no granular pigment	***Bjerkandera***
4	Distinctly hydnoid or dentate hymenophore	**5**
–	Smooth hymenophore, more or less	**6**
5	Basidiocarps pileate, spines regular conical	***Donkia***
–	Basidiocarps resupinate, spines irregular, dentate	***Pirex***
6	Dendrohyphidia, blue colors	***Terana***
–	No dendrohyphidia	7
7	Thick-walled, encrusted cystidia present	**8**
–	Cystidia absent or thin-walled	**10**
8	Basidiocarps pileate, encrusted cystidia deep-rooted, brown	***Porostereum***
–	Basidiocarps resupinate, cystidia more or less hyaline, not deep rooted	**9**
9	Tissue dense throughout, no rhizomorphs	***Phlebia unica***
–	Tissue loose, rhizomorphs present	***Rhizochaete***
10	Tissue dense throughout	***Phlebia* spp.**
–	Tissue loose	***Rhizochaete*** (incl. *Ceraceomyces* spp.)
11	Poroid species	**12**
–	Smooth or hydnoid species	**17**
12	Basidiocarps with encrusted, thick-walled subulate cystidia	**13**
–	Cystidia thin-walled and naked or lacking	**14**
13	Hyphal structure loose, basidiocarps pileate	***Oxychaete***
–	Hyphal structure dense, basidiocarps resupinate	***Phlebiopsis***
14	Basidiocarp with thick-walled conidia and often orange, anamorphic regions	***Riopa metamorphosa***
–	No conidia attached to basidiocarps, no separate anamorphic stage	**15**
15	Basidiocarp yellow, tramal tissue relatively dense	***Phanerina***
–	Basidiocarps whitish to buff, tramal tissue loose	**16**
16	Subicular hyphae regularly >5 µm in diameter, looking slightly inflated	***Phanerochaete***
–	Subicular hyphae mostly <5 µm in diameter, cylindrical	***Riopa pudens***
17	Hymenophore hydnoid	**18**
–	Hymenophore smooth	**19**

18 Spines small, their apices composed of heavily encrusted, cystidia-like hyphal endings ..... ***Hyphodermella***
– Spines not apically heavily encrusted..... ***Phanerochaete***
19 Tissue dense at least basally, subhymenium dense with no corymb-type branching, no rhizomorphs, cystidia very thick-walled, heavily encrusted (lamprocystidia)..... ***Phlebiopsis* or *Phaeophlebiopsis***
– Subicular tissue loose, subhymenium dense or loose corymb-type, rhizomorphs often present, thick-walled encrusted cystidia present or absent ... **20**
20 Subhymenium of the corymb-type, loose, rhizomorphs present or absent, no species with very thick-walled, heavily encrusted cystidia..... ***Phanerochaete***
– Subhymenial hyphae irregularly interwoven, basidiocarps pellicular, rhizomorphs always present, cystidia if present thick-walled, heavily encrusted, conical ..... ***Rhizochaete*** (see also *Phlebiopsis brunneocystidiata*, *P. laxa*)

Ceriporia pierii –group (Irpicaceae)

Ceriporia pierii and four closely related species described below seem to form a subclade of the large *Ceriporia* – *Leptoporus* clade (Figure 2). In morphological terms, the *C. pierii* group encompasses species with pale colored (white, pale pink or pale ochraceous), minutely rhizomorphic basidiocarps (Figure 10), and cylindrical to ellipsoid basidiospores normally exceeding 2 µm in width. In addition, fan-like crystal aggregations occur among hyphae (Figure 11g), and subicular hyphae are considerably wider than tramal and subhymenial ones. The latter feature is not unique for the *C. pierii* group but is found for instance in the genus type *C. viridans* and its closest relatives.

The *C. viridans* group is not very closely related to *C. pierii* and its sibling species (Figure 2), although morphological differences are very subtle. In the *Ceriporia viridans* complex the basidiospores are curved and mostly cylindrical, less than 2 µm in width (except *C. excelsa*), and hyphae possess more or less thickened walls (hyphal walls are thin in the *C. pierii* group). The *C. purpurea* and *C. spissa* species complexes have much brighter, red-colored basidiocarps, cylindrical spores, and hyphae of more or less equal diameter throughout the basidiocarp.

Morphologically species in the *C. pierii* group are very similar to each other, pore and spore characters being the most useful for identification (Table 4). ITS sequence differences are clear, 3.2–10.6% between species. Below is a general description for species in this group.

Description. Basidiocarps annual, resupinate, very thin (below 1 mm), 1–20 cm wide. Sterile margin byssoid, white to cream-colored, producing thin, white rhizomorphs (in all species but not all specimens). Pore surface pale-colored (white-yellow-pale ochraceous), pores shallow, uneven, angular, partly fusing together and even irpicoid, 2–6 per mm. Dissepiments mostly thin, wavy to dentate. Subiculum byssoid, white, very thin (up to 0.1 mm). **Hyphal system** monomitic, simple-septate. Subicular hyphae thin- to moderately thick-walled, branched at sharp angles, producing abundant H-like connections, always wider than

Table 4. Comparison of species in the *Ceriporia pierii* group.

Species	Distribution	Color of dry basidiocarps	Pores per mm	Basidiospores L×W
C. humilis	temperate Eurasia	white to cream-colored	5–6	narrowly ellipsoid to cylindrical 3.8×2.1 µm
C. mpurii	New Guinea	cream-colored to pale gray	5–6	ellipsoid to narrowly ellipsoid 3.4×2.2 µm
C. pierii	temperate Europe	cream-colored to rosy	2–3	ellipsoid to narrowly ellipsoid 4.7×2.8 µm
C. sericea	temperate East Asia	cream-colored to pale ochraceous	3–5	thick cylindrical 4.3×2.4 µm
C. sordescens	temperate Eastern North America	yellowish to dirty ochraceous	3–4	ellipsoid to narrowly ellipsoid 3.6×2.2 µm

tramal hyphae, 4–14 µm in diameter, with rare clamps. Tramal hyphae parallel, with thin or a bit thickened walls, some with H-connections, 2.6–5.3 µm in diameter. Crystals abundant among or on subicular/tramal hyphae, fan- or star-shaped, up to 20–30 µm in the widest dimension. Resinous, hyaline or yellowish matter present as small droplets among tramal hyphae. Subhymenial hyphae vertically arranged, short-celled, thin-walled, branched at sharp angles, 2.5–4.5 in diameter. Dissepiment edges sterile, consisting of tramal hyphal ends.

Cystidia absent.

Hymenium. Basidia clavate, 4-spored, 8.5–19×3.5–5.5 µm.

Basidiospores thin-walled, hyaline, thick-cylindrical to ellipsoid, about 3–5.5×2–3 µm.

Ecology. All the species produce basidiocarps on rotten, white-rot angiosperm wood.

***Ceriporia humilis* Spirin & Miettinen, sp. nov.**

MycoBank 811540

Figures 10b and 11a

Holotype. Russia. Nizhny Novgorod: Lukoyanov Dist., Sanki, *Quercus robur*, 14 Jul 2012, Spirin 4706 (H).

Etymology. *Humilis* (Lat.), simple, shy; refers to basidiocarps devoid of good characters.

Description. Basidiocarp 0.1–0.2 mm thick. Pore surface white to cream-colored, pores 5–6 per mm. Sterile margin narrow (up to 0.5 mm wide). Subicular hyphae irregularly arranged to subparallel, 4–8.3 µm in diameter. Tramal hyphae 4.1–5.3 µm in diameter. Subhymenial hyphae 3–4.7 µm in diameter. Basidia 9.2–13.3×4.2–5.1 µm. Basidiospores narrowly ellipsoid to cylindrical, ventral side flat, rarely concave, (3.1)3.2–4.2(5.0)×(1.8)1.9–2.2(2.3) µm, L=3.78 µm, W=2.09 µm, Q=1.81.

Remarks. *Ceriporia humilis* produces rather large basidiocarps with rhizomorphs at the marginal area or in the substrate. The type specimen was collected from a fallen oak log in Nizhny Novgorod Region, European part of Russia. Another, much older collection derives from Helsinki, Finland (HFR009978, a fallen log of *Acer*

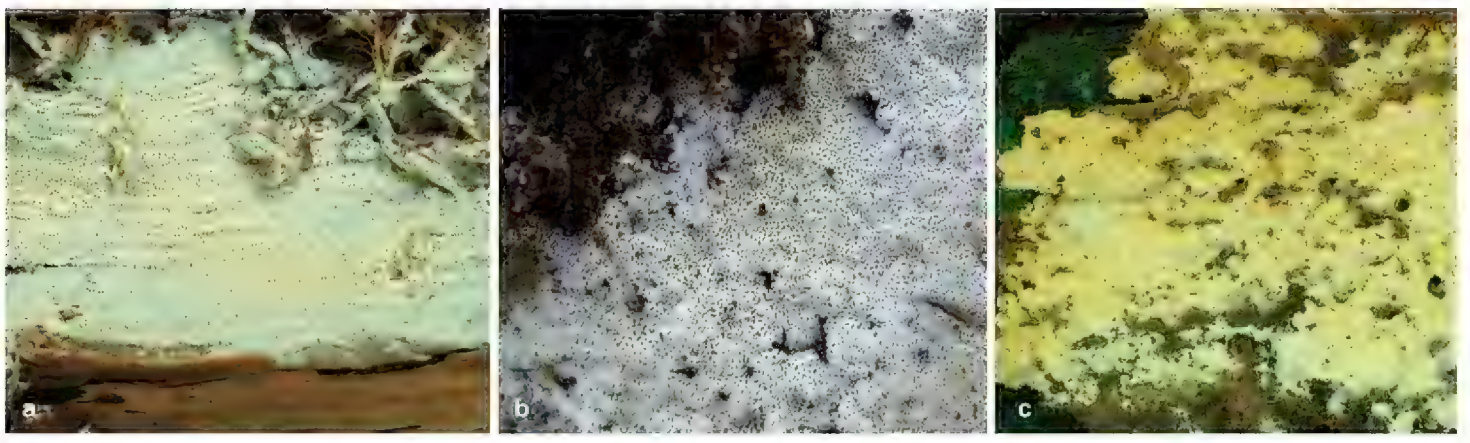

Figure 10. Fruiting bodies of species in the *Ceriporia pierii* group. **a** *Ceriporia mpurii*, holotype **b** *Ceriporia humilis*, holotype **c** *Ceriporia sordescens*, holotype. Photos taken in the field.

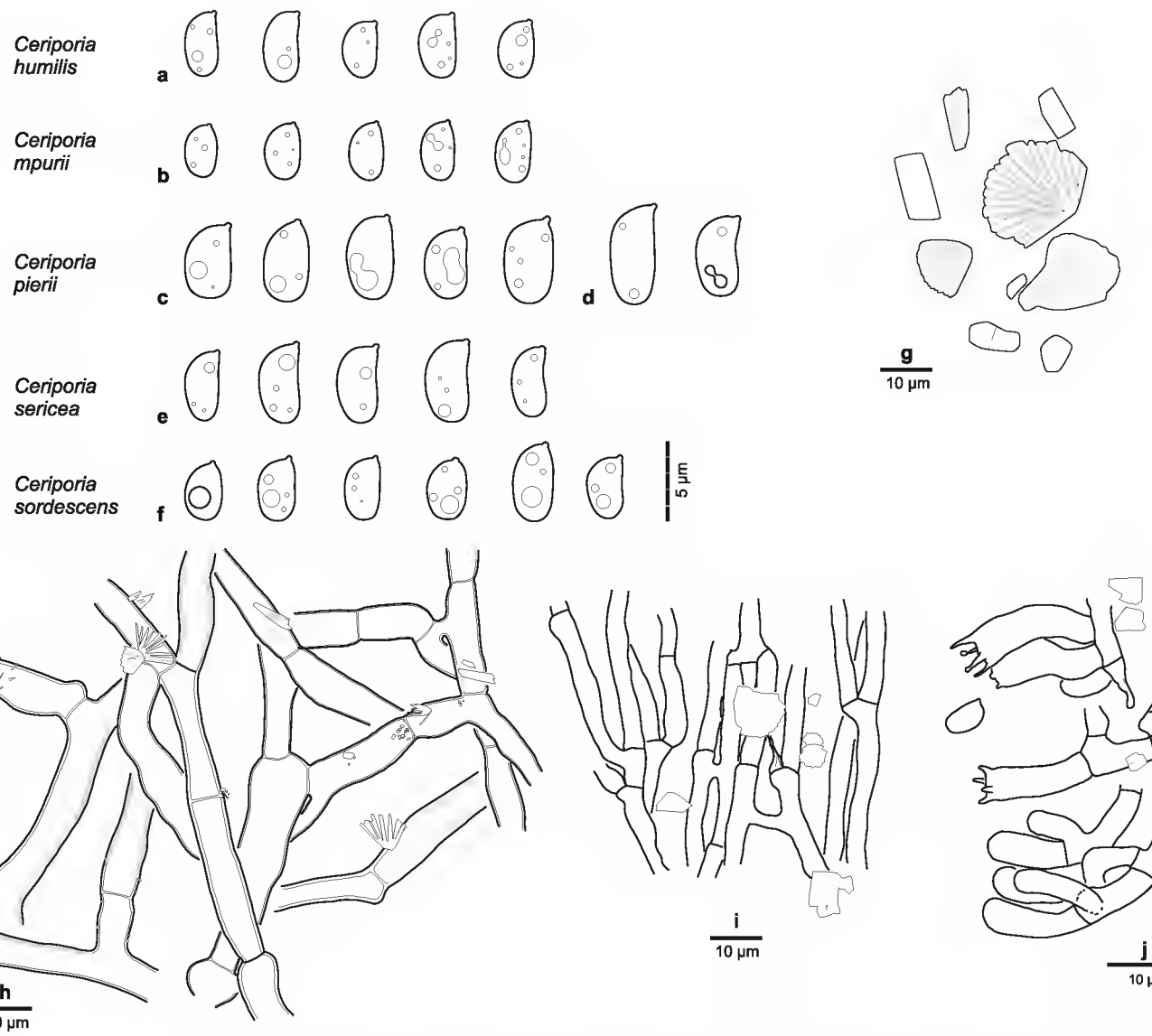

Figure 11. Microscopic characters in the *Ceriporia pierii* group. Spores of **a** *C. humilis*, holotype **b** *C. mpurii*, holotype **c** *C. pierii*, holotype **d** *C. pierii*, Rivoire 2378 **e** *C. sericea*, holotype **f** *C. sordescens*, holotype **g** Fan-shaped and rhomboidal crystals characteristic for the *C. pierii* group in *C. mpurii*, holotype. Hyphal structures of *C. pierii*, holotype: **h** subicular hyphae **i** tramal hypha **j** hymenial cells.

platanoides). One sequence of *C. viridans* in the INSDC from Shanxi, China belongs to *C. humilis* (KC182775, Dai 7642) showing that the species is present in East Asia, too. *Ceriporia humilis* has the narrowest spores in the whole species complex.

***Ceriporia mpurii* Miettinen & Spirin, sp. nov.**
MycoBank 811541
Figures 10a and 11b, g

Holotype. Indonesia. Papua Barat: Saukorem, Minjanbiat, -0.5755°: 133.1447°, lowland primary forest, fallen trunk of *Spondias* (40 cm in diameter, decay stage 4/5), 3 Nov 2010, Miettinen 14381 (H, ANDA, MKW).

Etymology. Named after mpur, the people and language spoken around the type locality.

Description. Basidiocarp 0.1–0.2 mm thick, up to 10 cm in the widest dimension. Pore surface cream-colored, in older parts with light gray hues, pores 5–6 per mm. Sterile margin narrow (up to 0.5 mm wide). Subicular hyphae irregularly arranged, 4.8–12.7 µm in diameter. Tramal hyphae 3.2–4.8 µm in diameter, in older parts glued together. Subhymenial hyphae 3–4 µm in diameter. Basidia 8.7–11.2×3.9–5.3 µm. Basidiospores ellipsoid to narrowly ellipsoid, ventral side mostly flat, very rarely slightly convex, (2.7)2.8–3.9(4.2)×2–2.3(2.4) µm, L=3.35 µm, W=2.15 µm, Q=1.55.

Remarks. *Ceriporia mpurii* is very similar to *C. humilis* (see above), differing in slightly darker color of the basidiocarps and a bit rounder spores. Moreover, hyphae in older parts of tubes are densely arranged and glued together, while they are loosely arranged in *C. humilis*. *Ceriporia mpurii* is known so far from its type locality in New Guinea.

***Ceriporia pierii* Rivoire, Miettinen & Spirin, sp. nov.**
MycoBank 811542
Figure 11

Holotype. France. Rhône-Alpes: Vernaison, *Populus nigra*, 24 Sep 1995, Rivoire 1161 (H, LY).

Etymology. Named after Max Pieri, who with Bernard Rivoire first discovered this species.

Description. Basidiocarp 0.2–1 mm thick, 1–4 cm in the widest dimension. Sterile margin narrow (up to 1 mm wide). Pore surface cream-colored to rosy, in well-developed basidiocarps with apricot tints, pores 2–3(4) per mm, dissepiments mostly entire. Subicular hyphae more or less parallel to substrate, (5)5.1–8.2(9.1) µm in diameter; a few hyphae bearing incomplete clamps or inflated portions. Tramal hyphae 4–5.2 µm in diameter. Subhymenial hyphae 2.9–4 µm in diameter. Basidia 13.8–19.3×4.4–5.2 µm. Basidiospores ellipsoid to rarely cylindrical, ventral side flat or slightly concave, (3.9)4.1–5.4(6.1)×2.4–3.1(3.2) µm, L=4.72 µm, W=2.77 µm, Q=1.70.

Remarks. *Ceriporia pierii* is introduced here to encompass *C. davidii* sensu Pieri and Rivoire (1997). Pieri and Rivoire identified *C. camaresiana* (Bourdot & Galzin) Bondartsev & Singer as the most similar species to *C. pierii*, but our data show that the two are not closely related (Figure 2). Basidiospores of *C. camaresiana* are clearly curved, mostly bean-shaped and longer, 5.26×2.74 µm (Table 5). Moreover, the hy-

Table 5. Spore measurement statistics of polypores. Bold-face values are composite statistics for species. L = average of spore length, W = average of spore width, Q = L/W, and n = number of spores measured. The whole range is given in parentheses; 90% range excluding 5% extreme values from both ends of variation is given without parentheses; in case the values are identical, parentheses are omitted.

Species	Length	L	Width	W	Q'	Q	n
Ceriporia camaresiana	**(4.6)4.7–6.2**	**5.26**	**2.4–3.0(3.1)**	**2.74**	**1.7–2.2(2.4)**	**1.92**	**30**
Ceriporia humilis	**(3.1)3.2–4.2(5.0)**	**3.78**	**(1.8)1.9–2.2(2.3)**	**2.09**	**1.5–2.1(2.3)**	**1.81**	**60/2**
holotype	(3.4)3.5–4.2	3.92	(1.8)1.9–2.2(2.3)	2.05	(1.6)1.7–2.1(2.3)	1.91	30
Kujala HFR009978	(3.1)3.2–4.2(5.0)	3.65	2.0–2.3	2.13	1.5–2.0(2.3)	1.71	30
Ceriporia mpurii	**(2.7)2.8–3.9(4.2)**	**3.35**	**2.0–2.3(2.4)**	**2.15**	**(1.3)1.4–1.8**	**1.55**	**50**
Ceriporia pierii	**(3.9)4.1–5.4(6.1)**	**4.72**	**2.4–3.1(3.2)**	**2.77**	**(1.4)1.5–2.0(2.3)**	**1.70**	**90/3**
holotype	(3.9)4.1–5.2(5.3)	4.65	2.6–3.1(3.2)	2.83	(1.4)1.5–1.8(1.9)	1.64	30
Rivoire 1822	4.1–5.2(5.3)	4.56	2.4–3.1(3.2)	2.73	1.5–1.8(1.9)	1.67	30
Rivoire 2378	(4.0)4.2–5.7(6.1)	4.94	2.4–3.1(3.2)	2.74	(1.5)1.6–2.3	1.81	30
Ceriporia sericea	**(3.8)3.9–4.8(5.2)**	**4.32**	**(2.1)2.2–2.7**	**2.38**	**(1.5)1.6–2.1**	**1.82**	**30**
Ceriporia sordescens	**(3.2)3.3–4.2(4.6)**	**3.61**	**(2.0)2.1–2.5(2.6)**	**2.24**	**1.4–1.8**	**1.61**	**30**
Hapalopilus eupatorii	**(3.3)3.4–4.5(5.2)**	**3.96**	**(2.2)2.4–3.1(3.2)**	**2.75**	**(1.2)1.3–1.6(1.9)**	**1.44**	**91/2**
holotype	3.3–4.5(4.8)	4.00	(2.2)2.3–3.1(3.2)	2.80	(1.2)1.3–1.6(1.7)	1.43	60
holotype of *Ceriporiopsis herbicola*	(3.5)3.6–4.5(5.2)	3.89	2.4–2.9	2.65	1.4–1.7(1.9)	1.47	31
Hapalopilus percoctus	**(3.7)3.8–4.6**	**4.11**	**(2.7)2.8–3.3**	**2.98**	**1.3–1.5(1.6)**	**1.38**	**30**
Hapalopilus ribicola	**(3.9)4.0–5.0(5.2)**	**4.36**	**(2.2)2.3–3.0(3.3)**	**2.66**	**(1.4)1.5–1.9(2.0)**	**1.64**	**90/3**
lectotype	(4.0)4.1–5.0(5.1)	4.37	2.2–3.0	2.55	1.5–1.9(2.0)	1.71	30
Alanko 145112	4.0–5.1(5.2)	4.43	(2.3)2.4–3.1(3.3)	2.76	(1.4)1.5–1.8(1.9)	1.60	30
Eriksson 1201	(3.9)4.0–4.8(5.0)	4.29	(2.3)2.4–3.0(3.1)	2.67	1.5–1.7	1.61	30
Hapalopilus rutilans	**(3.1)3.2–5.1(5.8)**	**4.00**	**(1.9)2.0–2.7(3.1)**	**2.30**	**(1.3)1.5–2.1(2.4)**	**1.74**	**400/13**
neotype	3.4–4.6(4.9)	4.00	(2.1)2.2–2.6(2.7)	2.37	1.4–1.9(2.0)	1.69	40
Haikonen 19509	(3.4)3.5–4.6(4.8)	4.00	1.9–2.4(2.6)	2.14	(1.6)1.7–2.1(2.2)	1.87	30
Haikonen 26561	3.1–4.2(4.3)	3.59	1.9–2.4(2.5)	2.18	1.4–2.0(2.1)	1.65	30
Kotiranta 18819	(3.4)3.5–4.2(4.3)	3.79	1.9–2.2(2.3)	2.09	1.6–2.1	1.81	30
Miettinen 14427	(3.8)3.9–5.3	4.50	2.0–2.4	2.20	(1.6)1.7–2.4	2.05	30
Miettinen 15793	(3.2)3.3–4.2(4.8)	3.72	1.9–2.3	2.12	1.5–2.2	1.76	30
Niemelä 6749	(3.8)3.9–4.6(5.7)	4.29	2.3–2.7(2.8)	2.52	1.5–1.9(2.2)	1.70	30
Niemelä 7134	(3.1)3.2–4.2(4.3)	3.52	2.0–2.4(2.5)	2.20	1.4–1.8	1.60	30
Niemelä 8896	(3.8)3.9–5.1	4.32	(2.2)2.3–2.8(2.9)	2.50	(1.5)1.6–2.0	1.73	30
Saarenoksa 28283	(4.0)4.1–5.0(5.3)	4.45	(2.2)2.3–2.8	2.47	1.6–2.1	1.80	30
Spirin 5968	3.2–3.9(4.1)	3.49	(2.0)2.1–2.4	2.22	1.4–1.7(1.8)	1.57	30
Oxychaete cervinogilva	**(5.9)6.0–8.4(8.9)**	**6.93**	**2.8–3.7(3.8)**	**3.17**	**(1.8)1.9–2.5(2.6)**	**2.19**	**60/2**
Curnow 3772	(5.9)6.0–8.0	6.66	2.8–3.7	3.07	1.9–2.5(2.6)	2.17	30
Schigel 5216	6.0–8.8(8.9)	7.20	(2.9)3.0–3.8	3.27	(1.8)1.9–2.5(2.6)	2.20	30
Phanerina mellea	**(5.2)5.8–7.2(7.8)**	**6.43**	**2.8–3.7(4.1)**	**3.19**	**(1.6)1.8–2.3(2.4)**	**2.02**	**100/4**
Miettinen 9134	(6.0)6.1–7.2(7.8)	6.48	(2.9)3.0–3.7(3.8)	3.20	1.7–2.3(2.4)	2.03	30
Miettinen 11393	(5.2)5.4–6.9(7.0)	6.20	2.8–3.2	2.98	(1.8)1.9–2.3(2.4)	2.08	30
Nuñez 503	(5.7)5.8–7.5(7.7)	6.49	(2.9)3.0–4.0(4.1)	3.33	(1.6)1.7–2.3(2.4)	1.95	30
Ryvarden 10519B	5.9–7.4	6.81	3.2–3.7	3.38	1.8–2.2	2.01	10
Riopa metamorphosa	**(4.2)5.0–6.6(8.2)**	**5.69**	**(2.0)2.2–3.1(3.5)**	**2.59**	**(1.7)1.9–2.6(2.8)**	**2.19**	**168/4**
epitype	5.2–6.6(6.8)	5.84	(2.1)2.3–3.0(3.1)	2.59	1.9–2.7	2.25	50

Species	Length	L	Width	W	Q'	Q	n
holotype of *Ceriporia davidii*	4.9–6.2(6.3)	5.51	2.3–3.0	2.68	1.9–2.3	2.05	30
Spirin 2395	5.0–7.6(8.2)	5.82	(2.0)2.1–3.3(3.5)	2.55	(1.8)1.9–2.7(2.8)	2.29	58
Spirin 2686	(4.2)4.6–6.2(6.5)	5.35	2.3–2.9(3.1)	2.59	(1.7)1.8–2.3(2.4)	2.07	30
Riopa pudens	**(4.2)4.3–5.6(6.2)**	**5.01**	**(1.8)1.9–2.2(2.3)**	**2.08**	**2.1–2.7(2.8)**	**2.41**	**40**

phal structure is different: in *C. camaresiana* hyphae are mostly long-celled and not inflated, covered with small resinous droplets, and their diameter is approximately the same in all parts of the basidiocarp (3–4 µm in trama and 4–5 µm in subiculum).

***Ceriporia sericea* Spirin & Vlasák, sp. nov.**
MycoBank 811543
Figure 11e

Holotype. Russia. Khabarovsk: Khabarovsk Dist., Malyi Niran, *Tilia amurensis*, 6 Aug 2012, Spirin 4944 (H).

Etymology. *Sericeus* (Lat.), silky, refers to the soft consistency of basidiocarp

Description. Basidiocarps 0.3–0.5 mm thick, up to 4 cm in the widest dimension. Margin narrow (up to 1 mm wide). Pore surface cream-colored to pale ochraceous, pores 3–5 per mm. Subicular hyphae subparallel, 4.4–9.4 µm in diameter, some inflated. Tramal hyphae 3.2–4.8 µm in diameter. Subhymenial hyphae 2.9–3.7 µm in diameter. Basidia 10.4–13.8×3.4–5 µm. Basidiospores thin-walled, hyaline, thick cylindrical, ventral side concave (bean-shaped), (3.8)3.9–4.8(5.2)×(2.1)2.2–2.7 µm, L=4.32 µm, W=2.38 µm, Q=1.82.

Remarks. *Ceriporia sericea* is characterized by soft, pale-colored, rhizomorphic basidiocarps and medium-sized, bean-shaped spores.

***Ceriporia sordescens* Miettinen & Spirin, sp. nov.**
MycoBank 811544
Figures 10c and 11f

Holotype. United States. New York: Essex Co., Huntington Wildlife Forest, Arbutus Lake, 43.9856° : -74.2469°, fallen dicot trunk (*Acer saccharum*?, 50 cm in diameter, decay stage 3/5), 18 Aug 2012, Miettinen 15492.2 (H).

Etymology. *Sordescens* (Lat.), becoming dirty-colored, refers to color change upon drying.

Description. Basidiocarps 0.2–0.5 mm thick, up to 20 cm in the widest dimension. Sterile margin up to 3 mm wide. Pore surface yellowish, in dry specimens pale to dirty ochraceous, in a few portions with pinkish hues, pores 3–4 per mm. Subicular hyphae subparallel, 5–13.6 µm in diameter, some inflated. Tramal hyphae 2.6–4 µm

in diameter. Subhymenial hyphae 2.5–4.6 µm in diameter. Basidia 10.1–18.4×4.1–5.2 µm. Basidiospores ellipsoid to narrowly ellipsoid, ventral side flat or slightly convex, very rarely slightly concave, (3.2)3.3–4.2(4.6)×(2.0)2.1–2.5(2.6) µm, L=3.61 µm, W=2.24 µm, Q=1.61.

Remarks. *Ceriporia sordescens* is a close relative of *C. pierii* differing by its ochraceous colors and smaller spores. We have studied one morphologically very similar specimen to *C. sordescens* from Ontario, Canada identified (incorrectly in our view) as *Poria griseoalba* by R.F. Cain (H ex TRTC 33465). It may represent yet another species in the *C. pierii* group, differing from *C. sordescens* mainly by its smaller pores 4–5 per mm, and longer, thick cylindrical spores 4.2–5.1×2–2.3 µm (n=30), L=4.54, W=2.15, Q=2.12. *Poria griseoalba* (Peck) Saccardo was described from Osceola, New York (Peck 1885) as having small-pored, grayish white basidiocarps, and Lowe (1966) placed it among the synonyms of *Poria rhodella* Fr. (= *Ceriporia viridans* s. lato). Even if Lowe's species concept was probably wider than today, *Poria griseoalba* belongs in the vicinity of *C. viridans* and is clearly not conspecific with *C. sordescens*.

Specimens examined

We studied specimens from herbaria H, O, K and LY, as well as specimens from the personal herbarium of Josef Vlasák (JV). Type specimens of species described here are omitted since their specimen information is found in the descriptions. Sequenced specimens are marked with an asterisk (*).

Australohydnum dregeanum. INDIA. Madhya Pradesh: Dhuma, *Boswellia serrata*, 6 Sep 1990, March & Tiwari IDF 223 (O, H).

Ceriporia camaresiana. FRANCE. Bouches-du-Rhône: Eygalières, *Viburnum tinus*, 26 Oct 1995, Rivoire 1233 (H*, LY).

Ceriporia humilis. FINLAND. Uusimaa: Helsinki, Laajasalo, *Acer platanoides*, 20 Oct 1963, Kujala (H, HFR9978).

Ceriporia pierii. FRANCE. Rhône-Alpes: Vernaison, *Populus nigra*, 14 Oct 2000, Rivoire 1822 (H, LY); Orlienas, hardwood, 18 Apr 2004, Rivoire 2378 (H, LY), dead *Funalia gallica* on *Fraxinus excelsior*, 3 Jan 2007, Rivoire 3052 (H, LY).

Ceriporia viridans. NETHERLANDS. Noord-Holland: Amsterdam, Sloterdijk, dicot, 23 Jun 2007, Miettinen 11701 (H*).

Emmia latemarginata. POLAND. Małopolska: Tarnów, Krzyskie Forest, *Quercus robur*, 4 Sep 1997, Piątek (H*).

Hapalopilus eupatorii. FRANCE. Seine-Maritime: Petit-Couronne, *Eupatorium cannabinum*, 1882 Letendre 19 (H 7008580, Karsten's herbarium 5927, lectotype of *Physisporus eupatorii* selected by Lowe 1956). Rhône: Vourles, *Robinia pseudoacacia* in *Renynoutria japonica* thicket, 3 Mar 2014, Rivoire 5333 (LY*). GERMANY. Nordrhein-Westfalen: Mönchengladbach, Volksgarten, *Reynoutria japonica* 04 Nov 2013, Bender (LY BR-5305*). UNITED KINGDOM. Oxfordshire: Henley

on Thames, *Arctium* sp., 10 Dec 2006, Fortey (holotype of *Ceriporiopsis herbicola* in K, isotype in O* studied).

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Supplementary material 1

S1 Table - INSDC accession numbers

Authors: Otto Miettinen, Viacheslav Spirin, Josef Vlasák, Bernard Rivoire, Soili Stenroos, David Hibbett

Data type: DNA sequence identifiers

Explanation note: INSDC accession numbers for DNA sequences used in this study. Specimens provided with collector and collection number information have been sequenced for this study, the rest retrieved from the INSDC database.

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